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THE GENUS GRIFFITHSIA (RHODOPHYCEAE) IN HAWAII

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The small, inconspicuous plants of the genus *Griffithsia* (Ceramiaceae, Rhodophyceae) are usually missed in general collections of algae. For the most part they are microscopic as well as epiphytic and occur well-mixed with other algae. In the subtropical waters of the Hawaiian Islands, members of this genus are usually found in reef and rocky shore habitats. They do not occur in abundance.

Griffithsia is fairly well known from the Atlantic and Indian Oceans, Caribbean and China Seas, and little known from the Pacific. The first record of the genus in the Hawaiian group was made by Reed in 1907, with reference to the economic use of the plants by the native Hawaiians. The algae are one of nearly seventy which were used to supplement the diet of the Hawaiians. Some of the more common native names of members of this genus are limu (literally translated as edible algae) moopuna-a-ka-lipoa, and limu aupuu. The native names of this and other algae vary from island to island, and sometimes on a single island.

Reinbold (1907) has listed *Griffithsia thyrsigera* (= *G. tenuis*) from Hawaii. MacCaughey (1917) and Neal (1930) have mentioned *Griffithsia ovalis* Harvey as possibly being present in the Hawaiian Islands.

Five species of *Griffithsia* are recorded here from the Hawaiian group. Four are listed for the first time from the area, and the presence of *G. ovalis* is confirmed.

New extensions of ranges are listed for *Griffithsia Binderiana* Sonder, an Australian species, *G. tenuis* C. Agardh, a cosmopolitan species, *G. Metcalfii* Tseng, reported from China, *G. ovalis* Harvey from Australia, and *G. rhizophora* Grunow from Ceylon, China, and the Malay Archipelago.

Cystocarps of *Griffithsia tenuis* and *G. Binderiana* are studied for the first time.

The following key is based on characters which are present for the greater part of the life history of the plants in the Hawaiian Islands. Cystocarpic and spermatangial plants which furnish the best differences among the species are infrequently found.

KEY TO THE SPECIES

A. Tetraspores between the articulations of the vegetative cells

B. Involucre surrounding tetraspores arising from vegetative cells; cells microscopic, subcylindrical below, globose at tips ..... **1. G. ovalis.**

B. Involucre attached to tetraspore pedicel; vegetative cells macroscopic and moniliform throughout ..... **2. G. Metcalfii.**

A. Tetraspores borne on specialized branches, or at the tips of the filaments

C. Cells cylindrical, slender; all reproductive structures formed on lateral pedicels ..... **3. G. tenuis.**

C. Cells subcylindrical or globose

D. Reproductive structures in lateral, specialized branches, all involucrate ..... **4. G. Binderiana.**

D. Tetraspores (other plants not seen) at the tips of globose cells; no involucre formed ..... **5. G. rhizophora.**

1. Griffithsia ovalis Harvey, Phycologia Australica **4**:203. 1862.

PLATE I, FIGS. 1–4; PLATE II, FIGS. 1–2

Plants in well-formed tufts to 2 cm. in height, or creeping on other algae and having erect filaments. Cells at the tips are oval to globular, 50–100 μ in diameter. Cells directly below are moniliform to subspherical, and at the base are larger and subcylindrical to ellipsoidal, 500–700 μ in diameter. Branches are occasionally fastigiate but predominantly dichotomous, with the tips slightly convergent. Rhizoids are commonly found throughout the plants which creep.

Tetrasporangia are borne between the articulations of the cells toward the tip, and are pedicellate with four or more sporangia on a pedicel. The mature tetrasporangia are about 40 μ in diameter. A slightly incurved involucre of 12–16 cells surrounds the tetraspores. No male or female plants have been collected.

Type locality: King George's Sound, Western Australia.

Distribution: Recorded previously only from Australia, and here recorded from the Hawaiian Islands.

Hawaiian specimens examined: **Oahu Island:** Kawela Bay, *Abbott 770b*, sterile on *Mesotrema*; Waimanalo, north of Makapuu Point, *Abbott 911a*, sterile on *Laurencia*; Diamond Head, below lighthouse, *Abbott 899a*, tetrasporic on *Halimeda*, *Abbott 900*, sterile on *Dictyosphaeria*; Waikiki, near marine laboratory, *Abbott 396*, *474*, *492*, *501* on *Sargassum*, *Abbott 502*, *504*, all tetrasporic.

The plants seem to be members of the *Griffithsia rhizophora-Schousboeicoacta* complex, and although they have many vegetative characteristics in common, studies of the male and female plants would be greatly desired.

Except for the small size of *G. ovalis*, the Hawaiian specimens also seem related to *Griffithsia corallinoides* (L.) Batters (*G. corallina* (Lightf.) C. Ag.). The involucrate tetrasporangial groups at the articulations are characteristic of both species.

The specimens have been collected on volcanic rock as well as on coral where they are much entangled with other small algae, chiefly *Centroceras clavulatum* (C. Ag.) Montagne and *Falkenbergia rufalanosa* Harvey. Although these collections have been made at different times of the year, only tetrasporic plants have been found.

2. Griffithsia Metcalfii Tseng, Papers Mich. Acad. Sci. Arts and Letters, **27**:111–116. 1942.

PLATE II, FIGS. 3–6

Plant caespitose, to 5 cm. in height, the fronds free at the outer ends, subdichotomous in the upper parts of the filaments. Cells are conspicuously moniliform, spherical, 500–700 μ in the terminal cells, largest in diameter through the center of the filaments, and subspherical to subcylindrical basally. Attachment is by large, stout, basal rhizoids. Tenacular cells often connect branches near the base of the plant with each other. Hair clusters are present in young specimens, and are quickly deciduous.

Spermatangial clusters are crowded between fertile vegetative cells below the terminal ends of the branches, and are not involucrate. Tetrasporangia bear a few involucre cells on the common pedicel. No cystocarpic specimens were collected.

Type specimen: C. K. Tseng 938 in the herbarium of Tseng, from Yenkehai, Hainan Island.

Hawaiian specimens examined: **Oahu Island:** Laie Bay at Makahoa Point, *Abbott 25*, tetrasporic, *Abbott 662*, spermatangial; *Richard Cowan*, 3 specimens from Nanakuli, tetrasporic; *Edna Fassoth*, from Waimanalo, sterile; *Reed*, without number, date, or locality, sterile.

This species compares very favorably with the type specimen. It is usually found with corallines in wave-swept areas about the Island of Oahu. The familiar *Griffithsia globulifera* Harvey of the Atlantic is related vegetatively to this species, but differs in branching and location of spermatangia. *Griffithsia rhizophora* Grunow of the Malayasian-Chinese coasts resembles *G. Metcalfii*, but is a smaller plant and has branches consistently convergent at the tips.

3. Griffithsia tenuis C. Agardh, Species Algarum **2**(1):131. 1828.

Griffithsia thyrsigera (Thwaites) Askenasy, Algae, *in* Forschungsreise S.M.S.Gazelle **4**:36, *pl.* 9, *figs.* 1–4. 1889.

Griffithsia sp. Neal, Hawaiian Marine Algae, Bishop Museum Bull. **67**:73–74. 1930.

PLATE III, FIGS. 1–7

Plant in freely branching loose tufts to 5 cm. in height, or prostrate and creeping on other algae. The multinucleate filaments are irregularly dichotomous, narrow in aspect, and non-forcipate. In the Hawaiian specimens, subsecund branches rarely occur and thus this character, so prominent in specimens from the Caribbean and China areas, is not a good one here. Cells of the filaments are cylindrical to subcylindrical, 60–80 μ in diameter, becoming smaller at the tips where they are surrounded by two or more clusters of hairs, the lower one long and six or more times dichotomous, the upper one short and quickly deciduous.

The asexual plants are usually found to be separate from the sexual plants, but in one collection tetraspores are found on the same plant as the cystocarps (*Abbott 472*). Tetraspores occur in whorls of 4–12 at the nodes of the upper filaments, each on a clavate or pyriform pedicel. Deciduous involucral cells infrequently surround the tetraspores of the Hawaiian specimens.

Cystocarps are lateral on a one-celled pedicel, surrounded by an involucre of 12–16 cells. The auxiliary cell of the carpogonium is cut off by the supporting cell as reported for *G. corallina* by Kylin (1916), and *G. Metcalfii* by Tseng (1942). Carpospores are formed by the repeated division of the auxiliary cell on its outer face. They are pyriform and are massed. Spermatangia are stalked, subcapitate, subglobose, without involucre, on lateral specialized branches.

Type locality: Venice.

Distribution: Widely distributed in warm to subtropical waters; in the Pacific area at points on the China coast, Fiji, and at Tutuila Island, Samoa.

Hawaiian specimens examined: **Oahu Island:** Laie Bay, *Abbott 485*, sterile; *Abbott 486*, tetrasporic; Waimanalo, 3 miles north of Makapuu Point, *Abbott 907a* on *Dictyota*, tetrasporic; Halona, *Abbott 300*, on *Microdictyon Setchellianum*, tetrasporic; Hanauma Bay, *Abbott 50*, tetrasporic, spermatangial; Wailupe, east of fishpond, *Abbott 808a* on *Dictyota*, sterile; Kaalawai, *Abbott 642*, on *Sargassum echinocarpum*, tetrasporic; Waikiki near marine laboratory, *Abbott 472*, tetrasporic and cystocarpic; *Abbott 491*, spermatangial, cystocarpic, tetrasporic; *Neal 23*, carpogonial, tetrasporic; Diamond Head, below lighthouse, *Abbott 839*, sterile, *Abbott 896a* on *Dictyota*, sterile, *Abbott 897a* on *Liagora*, tetrasporic; *G. P. Andrews* without collecting data, tetrasporic; Kawela Bay, *Abbott 732b* on *Padina*, sterile. **Maui Island:** *E. Bailey 7*, 5 specimens of which two are tetrasporic, others sterile.

The persistent dichotomous branching of the Hawaiian specimens is a very misleading character since *Griffithsia tenuis* of other writers is taxonomically characterized by having lateral, secund branches. One collection of fifteen sets shows the secund habit of the species. These plants were epiphytic on a small *Sargassum echinocarpum*, and on *Champia* sp. The Hawaiian specimens appear to be more narrow in the size of the cells and have smaller tetraspores than the Atlantic and China specimens. The specimens collected at Hanauma Bay, in addition, show only four tetraspores in a whorl at the nodes and the pedicels are not typically clavate or pyriform as in the Waikiki specimens. These differences, however, may perhaps be attributed to the tide pool habitat of the former.

The appearance of tetraspores and cystocarps on the same plant is not rare for the Ceramiales (see Kylin, 1928, Drew, 1944), but is newly reported for *G. tenuis*. Unfortunately, I have not studied the species cytologically.

4. Griffithsia Binderiana Sonder, Bot. Zeit. **3**:52, 1845.

Bornetia Binderiana (Sond.) Zanard., Iconogr. Phycol. Med.-Adr. **2**:45. 1865 (cited by Børgeson, F. Danske Vidensk. Selsk., Biol. Medd. **19**(10):16. 1945). (See other references for this species by Sonder in literature cited.)

PLATE IV, FIGS. 1–7

Plants tufted, to 4 cm. in height, much branched, subdistichous, dichotomous, furcate at the tips. Cells are subcylindrical, 300–500 μ in width, 2.5 to 3 times as long in the central parts of the filaments, cells becoming gradually smaller toward the terminal ends. Tetraspores are

borne on characteristic cuneate or ovoid, solitary, secund pedicels; the tetraspores are surrounded by a prominent incurved involucre. Tetraspores are 50–60 μ in diameter. Three or more tetrasporangia are clustered on a common stalk. Rhizoids occur chiefly in the basal parts, but in some ecological forms they may occasionally appear laterally throughout the plant.

Type locality: "ad litus occidentale Novae Holland."

Hawaiian specimens examined: **Oahu Island:** near Elk's club, Waikiki, *Abbott 467*, sterile; Laie Bay at Makahoa Point, *Abbott 468*, tetrasporic; *Abbott 659*, spermatangial; *Abbott 660*, cystocarpic; *Abbott 661*, tetrasporic; *J. T. Conover* at Barber's Point, tetrasporic; *R. S. Cowan* at Nimitz Recreation Beach, south Ewa, near Barber's Point, tetrasporic; *J. F. Rock* from Honolulu Harbor, sterile. **Maui Island:** Paia, *E. Bailey* without number, some tetrasporic, others sterile.

The prominent lateral branches bearing involucrate tetraspores are most characteristic of this species, and fortunately the cystocarpic and spermatangial plants also show this characteristic well. The development of the cystocarp follows that of *G. corallina*, *G. Metcalfii* and *G. tenuis*. Spermatangial and cystocarpic plants have been found in the winter months, the tetrasporic plants throughout the year. Spermatangial and cystocarpic plants are reported for the first time.

Griffithsia Binderiana seems to be related to the oriental *G. subcylindrica* Okamura, especially in the vegetative structure. The cells of the latter appear to be larger both in width and length. The Hawaiian plants compare favorably with Harvey's description of specimens of *G. Binderiana* from Rottnest.

5. Griffithsia rhizophora Grunow *ex* Weber-van Bosse, Siboga Expeditie. Monograph **59c**:313. 1923.

PLATE I, FIGS. 5–9

Frond to 2 cm. in height, caespitose. Branches are convergent at the tips, otherwise subdichotomous and erect, or creeping. The cells are moniliform except at the base where they are subcylindrical. The central cells of the filaments are 400–500 μ in diameter with the same length. Terminal cells are somewhat less than 100 μ, basal cells 500 μ in diameter and twice as long. Tetraspores without involucre.

Type specimen: Ferguson 316, in Algae of Ceylon.

Distribution: Ceylon, Hainan, Malaya.

Hawaiian specimens examined: **Oahu Island:** Laie Bay, *Abbott 466*, tetrasporic; Waimanalo, 3 miles north of Makapuu Point, *Abbott 909a* on *Dictyota*, sterile; *Abbott 910a* on *Padina*, sterile; Wailupe, east of fishpond, *Abbott 802a* on *Dictyota*, sterile; Diamond Head, below lighthouse, *Abbott 816a* on *Sargassum*, sterile; Kaalawai, *Abbott 663a* on *Padina*, sterile; Kawela Bay, *Abbott 715a* on *Halimeda*, sterile.

The regular subdichotomous branching and the convergent tips of this species separate it vegetatively from *Griffithsia Metcalfii*. The latter plant is also larger. Of the Hawaiian species of *Griffithsia* studied, this

one is least known since only one fertile specimen was collected. The identification, therefore, should be considered to be tentative.

Griffithsia rhizophora was named by Grunow on a herbarium sheet (*nomen nudum*). Later, Madame Weber-van Bosse published it in the list of Siboga Algae, crediting it to Grunow. Article 48, section 7 of the International Rules states the ". . . name of the latter author must be appended to the citation with the connecting word *ex.*" The listing of the species should be as above.

The writer wishes to thank Dr. George F. Papenfuss of the University of California who has helped greatly in checking literature she was not able to see.

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PLATE I

All figures are drawn with the aid of a camera lucida. Each unit of scale A equals 200 μ; scale B, 100 μ; scale C, 50 μ; scale D, 10 μ.

Griffithsia ovalis Harvey. Figs. 1–4.

1. Vegetative cells with involucrate tetrasporangia between the articulations. (Scale B)
2. Habit of repent specimen showing rhizoid. (Scale A)
3. Involucrate tetrasporangia near tip of plant. (Scale B)
4. Mature tetrasporangium on a pedicel. (Scale D)

Griffithsia rhizophora Grunow *ex* Weber-van Bosse. Figs. 5–9.

5. (Upper figure) Mature tetrasporangia. (Scale D); (lower figure) tetrasporangia on pedicel. (Scale C)
6. Habit of typical specimen with forcipate tips. (Scale B)
7. Habit of repent specimen with rhizoids. (Scale C)
8. Tetrasporic plant. (Scale C)
9. Habit of specimen with nearly straight tips. (Scale B)

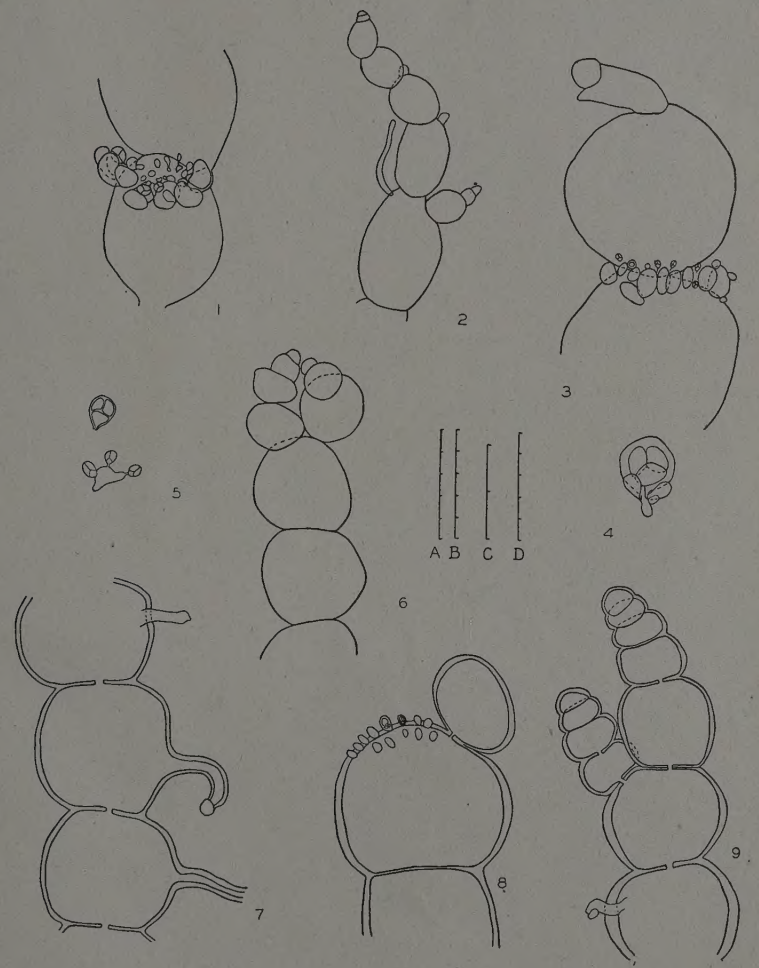

PLATE I

PLATE II

All figures are drawn with the aid of a camera lucida. Each unit of scale A equals 200 μ; scale B, 100 μ; scale D, 10 μ.

Griffithsia ovalis Harvey. Figs. 1–2.

1. Habit of erect specimen showing fastigiate branching. (Scale A)
2. Habit of creeping specimen showing secund branching. (Scale A)

Griffithsia Metcalfii Tseng. Figs. 3–6.

3. Tetraspores between articulations of vegetative cells. (Scale B)
4. Tip of a frond. (Scale B)
5. Spermatangial cluster. (Scale D)
6. Tetrasporic cluster. (Scale D)

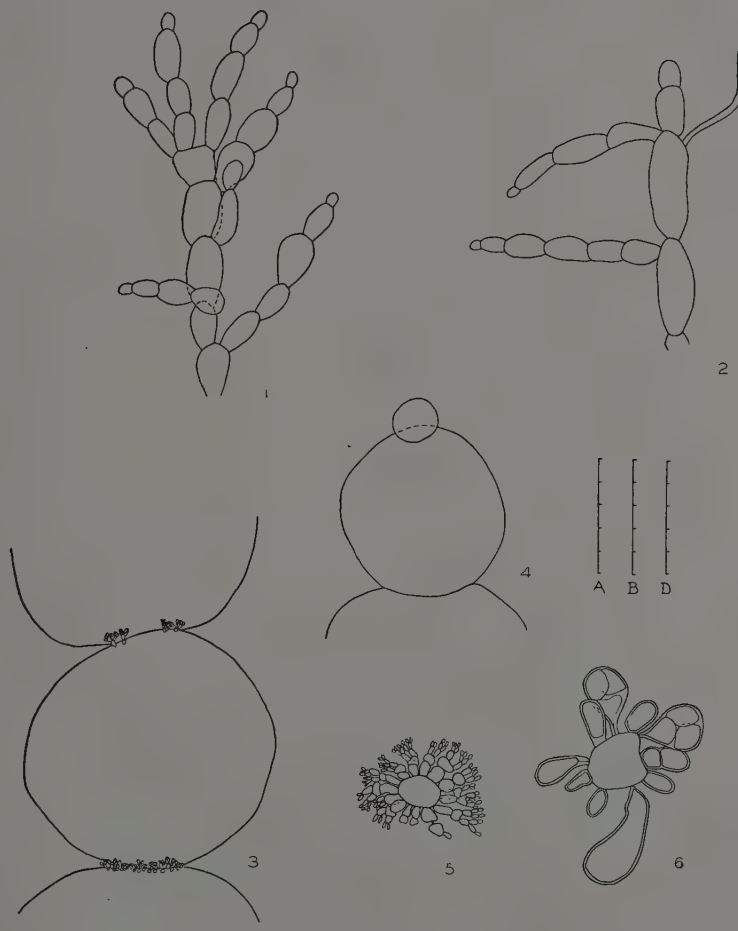

PLATE II

PLATE III

All figures are drawn with the aid of a camera lucida. Each unit of scale B equals 100 μ; scale C, 50 μ; scale D, 10 μ.

Griffithsia tenuis C. Agardh. Figs. 1–7.

1. Whorl of four tetrasporangia. (Scale C)
2. Habit of specimen with male cluster. (Scale B)
3. Spermatangial cluster. (Scale D)
4. Habit of robust specimen, showing young tetraspore. (Scale C)
5. Part of cystocarp, showing supporting cell derivatives and pyriform carpospores. (Scale D)
6. Involucrate cystocarp on lateral pedicel. (Scale C)
7. Young gonimoblast with involucre. (Scale D)

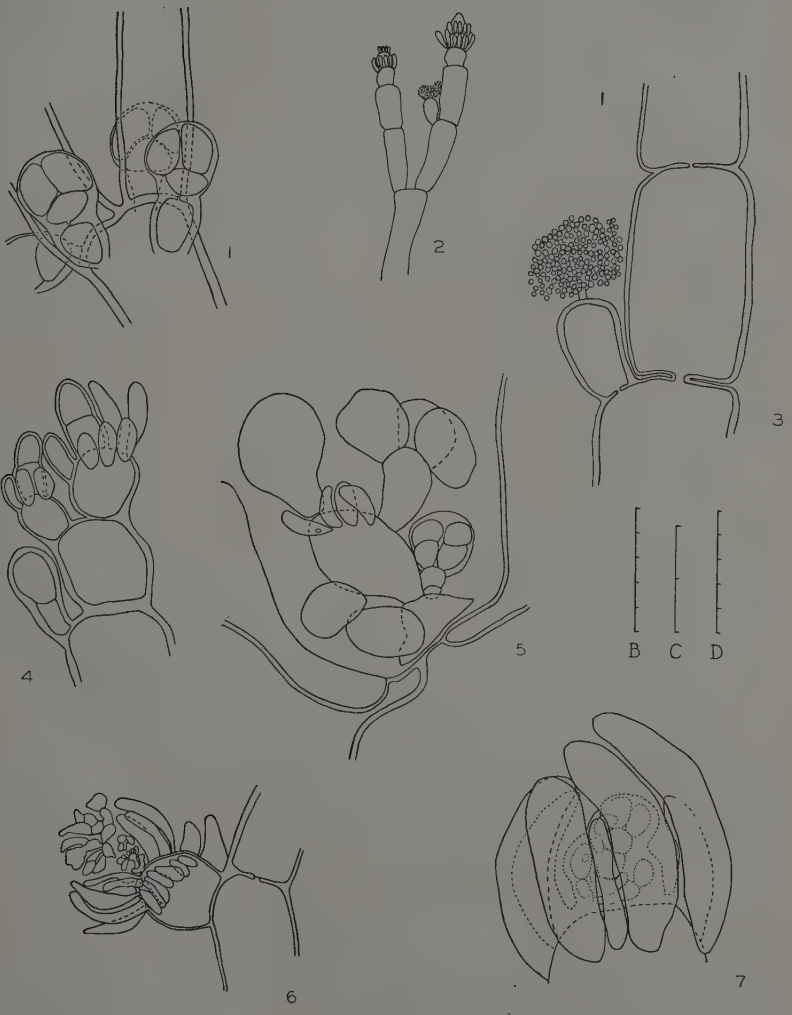

PLATE III

PLATE IV

All figures are drawn with the aid of a camera lucida. Each unit of scale B equals 100 μ; scale C, 50 μ; scale D, 10 μ.

Griffithsia Binderiana Sonder. Figs. 1–7.

1. Habit of portion of tetrasporic plant. (Scale B)
2. Spermatangial cluster with young involucre. (Scale D)
3. Spermatangial cluster on lateral pedicel, with surrounding involucral cells. (Scale B)
4. Detail of mature cystocarp showing a few carpospores. (Scale C)
5. Tetrasporic plant with involucrate tetrasporangia. (Scale B)
6. (a) Young tetraspore; (b) mature tetrasporangium showing pedicel. (Scale D)
7. Position of cystocarp with regard to involucre on a lateral pedicel. (Scale B)

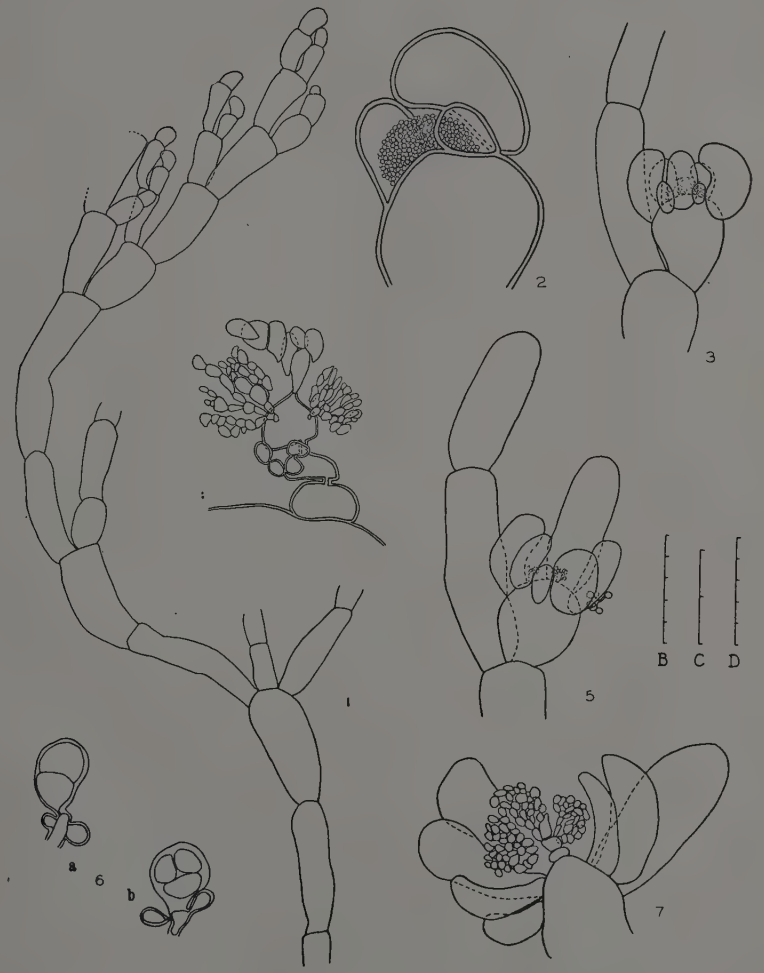

PLATE IV

2(4):455–473 FARLOWIA JULY, 1946

FUNGI DOMINGENSES NOVI VEL MINUS COGNITI. I.

CARLOS E. CHARDON

From May to November 1937, the writer was engaged by His Excellency President Rafael L. Trujillo as head of a party in charge of a partial survey of the natural resources of the Dominican Republic. Ample travel facilities, which permitted him to cover most of the territory of that country, were generously placed at his disposal.

A particularly interesting trip which lasted seven days was made on horseback from Jarabacoa to San José de Ocoa, in the company of Prof. H. A. Meyerhoff. The trail, which reaches an altitude of 2,400 meters, leads across the Cordillera Central through large and little-explored pine forests. A delightful temperate climate prevailed in these mountains and several days were spent botanizing in this *terra incognita* to mycology. Frequent collections were also made as time permitted, in other sections of the country. In short, close to a thousand specimens of fungi were collected which were sent to Prof. H. H. Whetzel to be added to the collections from the Dominican Republic previously made by M. F. Barrus, F. D. Kern, R. A. Toro, and the writer, and deposited in the herbarium of the Department of Plant Pathology, Cornell University.

The present contribution to the fungous flora of the Dominican Republic represents an addition of forty-four species, of which fourteen are apparently new to science. The writer wishes to acknowledge his thanks to the late Prof. H. H. Whetzel, of Cornell University, for encouragement and helpful suggestions; to Dr. Fred J. Seaver, of the New York Botanical Garden, for the determination of the Discomycetes and Hypocreales; and to Miss Edith K. Cash, of the U. S. Department of Agriculture, for contributing the description of a new species of the Phacidiales.

PEZIZALES

In Ciferri's "Micoflora Domingensis" (2) there are reported only three species of Discomycetes proper, all of which are common and well-known tropical forms. Ciferri's record is based on the paper published by Berkeley in 1852, "Enumeration of some fungi from Santo Domingo" (1), which was the first contribution published on the fungous flora of the Dominican Republic. The species are: *Cookeina sulcipes* (Berk.) Kuntze, *Cookeina tricholoma* (Mont.) Kuntze, and *Phillipsia domingensis* (Berk.) Berk.

Since the appearance of Berkeley's paper, ninety-two years ago, and in spite of the intensive collections made in the last twenty years by half a dozen explorers, not a single cup-fungus has been added to Berkeley's original list. This group of fungi has been overlooked because of its sapro-

phytic nature, the former mycologists having been interested in parasitic forms only.

We have made an effort to collect cup-fungi and have contributed thirteen specimens, representing nine different species, of which seven are new to the flora, and one is new to science. All the Discomycetes included below were determined by Dr. Fred J. Seaver, of the New York Botanical Garden.

This brings the total of known Pezizales in the Dominican Republic to ten species. In Puerto Rico, the number of species of this group reported by Seaver and Chardon (4) is forty-seven. Our list, consequently, is a mere beginning and could be multiplied many-fold by subsequent explorations.

The most common species found was the cosmopolitan *Cookeina sulcipes* forming beautiful conspicuous cups on dead sticks and debris in the shade. Cacao plantations furnish ideal conditions for its growth and the cups are found by the hundreds. *Cookeina tricholoma* and *Phillipsia domingensis* require the same habitat but are far less common.

The attractive *Ascobolus magnificus*, common in Puerto Rico, was encountered twice, always on dung, in the shade. *Erinella calospora* and *E. longispora* were both found on the bark of trees in the tropical region.

All the other species were found at much higher altitudes. On our trip to Constanza Valley, at the high point in Loma Barrero, along the trail just above Jarabacoa, we found two specimens on dung in a forest: *Ascophanus granulatus* and *Patella theleboides*. The altitude was 1150 meters. Further along, a third species was found, *Saccobolus Kerverni*. All these species are almost exclusively temperate species.

At Valle Nuevo, at an altitude of 2250 meters, where intense cold was felt all the time, we found *Patella coprinaria* on dung in the meadows near an old abandoned hut. This is the highest station at which a Discomycete has been found in the West Indies. This is also a temperate-zone species. It is not known in the tropical and subtropical zones, except for a single collection in the Luquillo Mountains of Puerto Rico.

Ascobolus magnificus Dodge, Mycologia **4:** 218. 1912.

First described from Puerto Rico, where it is common on cow dung. Also known from the Cauca Valley (Colombia) and New York City, where it has been cultivated in damp-chambers. Careful search for this species was rewarded by the collection of two specimens. The cup-shaped apothecia with the dark violet hymenium at maturity are typical.

On cow dung, Prov. Samana, in forests at Sabana la Mar, *Chardon 703*, July 5, 1937; Prov. La Vega, in shaded places near Jarabacoa, *Chardon 1136*, Sept. 13, 1937.

Ascophanus granulatus (Bull.) Speg., Michelia **1:** 235. 1879.

Small apothecia, 1–2 mm. in diameter, pale orange, with the concave hymenium orange. A common temperate-zone species.

On cow dung, Prov. La Vega, trail from Jarabacoa to Constanza, 1100–1200 m., *Chardon 1139*, Sept. 13, 1937.

Cookeina sulcipes (Berk.) Kuntze, Rev. Gen. Pl. **2:** 849. 1891.

One of the commonest and most conspicuous cup-fungi in the American tropics; also known from Australia. The cups are deep orange to rose color, attaining a diameter of 2 cms. or more. Specimens nos. *722* and *735* were collected among many hundreds of cups found in a well-sheltered cacao plantation, where moisture and shade afforded ideal conditions for development. Again at El Hatillo (specimen no. *1117*) the cups were very abundant, literally covering portions of the floor of a dense, humid forest.

On dead wood and forest debris, Prov. Samanas, Cacao plantations near Sabana la Mar, *Chardon 722* & *735*, July 5, 1937; Cacao plantations above Samana, Peninsula de Samana, *Chardon 739*, July 6, 1937; Prov. La Vega, forests at El Hatillo, *Chardon 1117*, Aug. 28, 1937.

Cookeina tricholoma (Mont.) Kuntze, Rev. Gen. Pl. **2:** 849. 1891.

Also known throughout the American tropics and Old World tropics. Of less frequent occurrence than the preceding species, the specimen cited below consisting of three apothecia. Cups red or deep red, externally clothed with long hairs.

On dead wood, Prov. La Vega, forests at El Hatillo, *Chardon 1231*, Aug. 28, 1937.

Erinella calospora Pat. & Gaill., Bull. Soc. Myc. Fr. **4:** 101, 1889.

On living bark of *Jambos*, Prov. La Vega, forests at El Hatillo, *Chardon 1231*, Aug. 28, 1937.

Erinella longispora (Karst.) Sacc., Syll. Fung. **8:** 507. 1889.

On dead wood, Prov. La Vega, forests, road to Cotui, *Chardon 975*, Aug. 6, 1937.

Saccobolus Kerverni (Crouan) Boudier, Ann. Sci. Nat. Ser. V. **10:** 229. 1869.

This species, with the exception of a single collection from Puerto Rico, occurs in the temperate regions of the world. It is common throughout North America and Europe, and is also found in Bermuda.

On cow dung, Prov. La Vega, trail from Jarabacoa to Constanza, 1100–1200 m., *Chardon 1140*, Sept. 13, 1937.

Patella coprinaria (Cooke) Seaver, N. Amer. Cup-Fungi 171. 1928.

Apothecia small, 2–3 mm. in diameter, bright yellow in color, bordered with hairs. This is a temperate-zone species, occurring in the United States and Europe. Its appearance in the temperate zone of Hispaniola may be significant in elucidating problems of geographical distribution.

On cow dung in meadows, Prov. La Vega, Valle Nuevo, above Constanza, Cordillera Central, 2250 m., *Chardon 1227*, Sept. 16, 1937.

Patella theleboides (Alb. & Schw.) Seaver, N. Amer. Cup-Fungi, 170. 1928.

Apothecia densely crowded, small, 2–3 mm. in diameter, bright yellow. Another temperate-zone species, reported in the United States, from Connecticut and Delaware to California; also in Europe.

On cow dung in the shade, Prov. La Vega, trail from Jarabacoa to Constanza, 1100–1200 m., *Chardon 1140*, Sept. 13, 1937.

PHACIDIALES

Nymanomyces Xolismae Cash sp. nov.

FIGURES 1–4

Stromata sparsa, atra, pulvinata, subcarbonacea, subcircularia, 2–3 mm. in diam., epidermicalia, amphigena; ascomata hypophylla, singularia, subcircularia, 1–2 mm. in diam., rima longitudinali vel lobis pluribus aperientia, hymenio brunneo; asci elongato-clavati, octospori, 100–150 x 18–25 μ; ascosporae elongato-ellipsoideae vel subclavatae, 1–3-seriatae, viridi-brunneae, 25–32 x 5–6 μ; paraphyses filiformes, subhyalinae; hypothecium atrum, plectenchymaticum, margine incrassato; pycnidia amphigena, loculata; pycnosporae parvae, hyalinae, ellipsoideae, 1.5–2 x 0.7 μ.

Stromata sparse, black, subcarbonaceous, round to angular, 2–3 mm. in diameter, or occasionally elongate and up to 5 mm. long, pulvinate, amphigenous, developing in the epidermis, surrounded on the lower surface by a broad, pale reddish, circular area, epiphyllous stromata sterile or pycnidial only; ascomata hypophyllous, single, subcircular, elliptical, or elongate, 1–2 mm. in diameter, opening by a longitudinal slit or more often by several lobes, the covering layer later breaking up and falling away, hymenium dark brown; asci long-clavate, gradually narrowed to a long pedicel, rounded at the apex, 8-spored, 100–120 (–150 x 18–20 (–25) μ; ascospores unicellular, narrow-ellipsoid or subclavate, sometimes slightly constricted near the center, obliquely uniseriate below, irregularly 2–3-seriate above, greenish-brown, the granulose contents occasionally containing one or two large hyaline guttules, 25–32 x 5–6 μ; paraphyses filiform, numerous, subhyaline to pale brownish, longer than the asci; hypothecial layer narrow, black, plectenchymatic, dense, and very much thickened toward the margin. Pycnidia amphigenous, when hypophyllous developing from the same stromata as the apothecia, irregularly chambered, the locules frequently becoming confluent and extending over most of the surface of the stroma; spores minute, hyaline, ellipsoid, filling the locules, 1.5–2 x 0.7–1 μ, emerging through irregular fissures and forming a white mass on the surface of the stroma; conidiophores not seen.

On *Xolisma* sp. (det. N. Y. Bot. Garden), Valle Nuevo, above Constanza, Prov. La Vega, Sept. 16, 1937, no. *1189* (**type**) and Sept. 17, 1937, *Carlos E. Chardon 1195*. Type specimen in the Mycological Collections of the Bureau of Plant Industry, Beltsville, Maryland; at Cornell University and in Chardon herbarium.

The only similar species described on an ericaceous host is *Criella leucothoes* P. Henn., which occurs in Brazil on an undetermined species of *Leucothoe*. No specimens of this species were available for comparison, but it appears to differ from the fungus on *Xolisma* in the epiphyllous stromata and much broader spores.

HYPOCREALES

Cordyceps militaris (L.) Link, Handb. **3**: 347. 1833.

On pupa of an insect, Prov. Monte Cristi, forests back of Copey, *Chardon 520*, June 8, 1937.

Hypocrea citrina (Pers.) Fries, Summa Veg. Scand. p. 185. 1849.

On dead wood, Prov. La Vega, trail from Maimón to Yuna River, *Chardon 1030*, Aug. 13, 1937.

Hypocrea patella Cooke & Peck; Peck, Ann. Rep. N. Y. State Mus. **29:** 57. 1878.

On dead wood, Prov. La Vega, road to Cotui, *Chardon 966*, Aug. 6, 1939.

Hypocrea rufa (Pers.) Fries, Summa Veg. Scand. p. 383. 1849.

On dead wood, Prov. La Vega, road to Bonao, *Chardon 797*, July 18, 1937.

Stilbocrea hypocreoides (Kalchbr. & Cooke) Seaver, Mycologia **2:** 62. 1910.

Sphaerostilbe hypocreoides Kalchbr. & Cooke, Grevillea **9:** 26. 1880.
Sphaerostilbe intermedia Ferd. & Winge, Bot. Tidssk. **29:** 12. 1908.

On dead wood, Prov. Monte Cristi, forests back of Copey, *Chardon 520*, June 8, 1937.

DOTHIDEALES

Dothidella domingensis Chardon sp. nov.

FIGURES 9–13

Stromata semper amphigena, atra, crustosa, conspicua, supra superficiem folii elevata, fere rotundata, 1 mm. diam., partem magnam folii tegentia, dothideacea (e cellulis distinctis fuscis composita); loculi 2–7 in quoque stromate, globosi, 96–120 μ diam.; asci clavato-cylindracei, octospori, 107–124 x 15–18 μ; sporae apice et basi monostichae, medio distichae, uniseptatae, hyalinae, longe ellipsoideae, una cellula majore obtusa, altera minore subacuta, 24–27 x 7–8 μ, leves, sine tunica crassa; paraphyses carentes.

Stromata amphigenous only, black, crust-like, conspicuous, raised above the surface of the leaves of the host, approximately circular, 1 mm. in diameter, covering a large portion of the leaf, dothideaceous (made up of distinct, dark-brown cells); locules several, 2–7 in each stroma, globose, 96–120 μ in diameter; asci cylindrical-clavate, 8-spored, 107–124 x 15–18 μ, with the spores uniseriate at the top and bottom, biseriate in the main body of the ascus; spores 1-septate, hyaline, long-elliptical, with one cell larger and with an obtuse end, the other cell smaller with a subacute end, 24–27 x 7–8 μ, surface smooth, without a thick cell wall; paraphyses absent.

The fungus looks superficially like *Dothidella tinctoria* (Tul.) Sacc., common on Compositae in the upper subtropical and temperate zone of the Andes of Venezuela and Colombia. In fact it looked identical to us, until a microscopic study disclosed that it was a new species. The spores were in asci (which is rarely observed in *D. tinctoria* where the spores are loose from a very early stage). The ascospores are also different; they are hyaline, 1-septate, with two unequal cells, and no thick cell wall was found. In *D. tinctoria* the cells are equal, the spores larger, 26–30 x 5–6 μ, the contents granular, and a thick cell wall envelops the ascospore.

For the marked differences cited above, reference is made to Figures 12 and 13.

On *Baccharis myrsinites* (Lam.) Pers., along trail from Jarabacoa to Constanza, Cordillera Central, 1300 m., *Chardon 1142*, Sept. 13, 1937 (**type**).

Trabutia conica Chardon, Mycologia **13:** 292. 1921.

The type is *Whetzel & Olive 658*, from Mayaguez, Puerto Rico, on *Drepanocarpus lunatus*, with which our material compares well. The species is known to occur also in Venezuela (*Chardon & Toro 474*), on *Lonchocarpus punctatus*. Not known elsewhere. The stromata are typically conical, epiphyllous, circular, about 1 mm. across, black, shiny, uniloculate, located between the cuticle and the epidermis. Spores globose, 9–11 μ, inordinately placed in the ascus.

On *Drepanocarpus lunatus* (L.f.) G. Meyer, Prov. Puerto Plata, road to Blanco, *Ciferri 4871*, June 15, 1931 (in Chardon's herb.).

Trabutia Danthoniae Chardon sp. nov.

Stromata atra, graminicola, linearia, 1 mm. longa, 0.5 mm. lata, interdum confluentia longioria et leviter elevata, subcuticularia; loculi 1–2 in quoque stromate, applanato-lenticulares, 150–240 x 74–90 μ, primo stylosporas longas, filiformes, 25–28 x 1 μ, posterius ascos gignens; asci clavati, octospori, 70–85 x 17–21 μ; sporae distichae, hyalinae usque subhyalinae, continuae, longe ellipsoideae, apice subacuto, 19–25 x 7–9 μ; paraphyses praesentes.

Stromata small, black, graminicolous, linear, 1 mm. long, 0.5 mm. wide, sometimes confluent and forming longer stromata slightly raised, subcuticular; locules 1–2 in a stroma, flat-lenticular, 150–240 x 74–90 μ, giving rise first to long, cylindrical stylospores, 25–28 x 1 μ, later to asci; asci clavate, 8-spored, 70–85 x 17–21 μ, with the spores biseriate; spores hyaline to subhyaline, 1-celled, long ellipsoidal with one end subacute, 19–25 x 7–9 μ; paraphyses present.

This interesting species forms inconspicuous stromata on a grass which is peculiar to and widespread in the higher elevations of the Cordillera Central. The subcuticular character of the stroma makes the fungus fall under *Trabutia*.

On *Danthonia domingensis* Hack. and Pilger, Prov. Azua, trail from Valle Nuevo to Rio de las Cuevas, Cordillera Central, 1770 m., *Chardon 1200*, Sept. 17, 1937 (**type**).

Phaeotrabutia Smilacis Chardon sp. nov.

Stromata epiphylla, rotundata, nigra, lucida, conspicua, 1–3 mm. diam., inter cuticulam et epidermidem folii definite insidentia; loculi generaliter singuli, applanati, 650–720 x 85–95 μ, supra clypeo denso atro, infra membrana tenui stromatica, brunnea praediti, interdum loculi 2–3, 320–410 x 80–90 μ; asci clavati usque cylindro-clavati, octospori, 123–135 x 29–38.5 μ; sporae in parte praecipua asci distichae, continuae, clare brunneae, ellipticae, 19–25 x 8.5–11 μ; paraphyses filiformes.

Stromata epiphyllous, circular, black, shiny, conspicuous, 1–3 mm. in diam., distinctly located between the cuticle and the epidermis of the leaf; locule single, flattened, 650–720 x 85–95 μ, with a heavy black clypeus above and a thin, brown, stromatic tissue below, sometimes divided into 2 or 3 locules, 320–410 x 80–90 μ; asci clavate to cylindric-clavate, 8-spored, 123–135 x 29–38.5 μ, with the spores biseriate in the main body of the ascus; spores 1-celled, distinctly brown, elliptical, 19–25 x 8.5–11 μ; paraphyses present, filiform.

The genus *Phaeotrabutia* was recently erected by Dr. Carlos Garcés Orejuela (Caldasia No. **2:** 77. 1941) to take care of species like *Trabutia*, possessing brown spores. In our Dominican material, the stromata lie between the cuticle and the epidermis, and the spores are unicellular, distinctly brown in color.

On *Smilax coriacea* Spreng., Prov. Azua, trail from Valle Nuevo to Río de las Cuevas, Cordillera Central, 1600 m., *Chardon 1202*, Sept. 17, 1937 (**type**).

Catacauma Sabal Chardon sp. nov.

FIGURES 14–17

Stromata amphigena, in utraque superficie folii pariter visibilia, angulata, leniter elevata, sordide brunnea, conspicua, 2–3 mm. longa (axe principali axem folii sequenti), 1.5 mm. lata, subter epidermidem in maturitate distincte visibilem evoluta, mesophyllum penentrantia; loculi plures, magni, 250–420 x 93–120 μ, applanati usque labyrinthiformes, supra clypeo atro denso praediti, infra et lateraliter sine membrana stromatica; asci clavati, octospori, exigue pedicellati, 68–85 x 35–43 μ; sporae in ascis irregulariter conglobatae, continuae, hyalinae, naviculares, 28–30 x 10–12 μ, subgranulosae; paraphyses filiformes, rarae.

Stromata amphigenous, equally visible on both surfaces of the leaves of the host, angular, slightly raised, dirty brown in color, conspicuous, 2–3 mm. long (with the main axis following that of the leaf), 1.5 mm. in width, originating beneath the epidermis, and in mature stromata the epidermal layer clearly seen above, not penetrating the mesophyll; locules several, large, 250–240 x 93–120 μ, flattened to labyrinthiform, with heavy black clypeus above and no stromatic tissue below or on the sides; asci clavate, 8-spored, short-pedicellate, 68–85 x 35–43 μ, with the spores irregularly pressed in the ascus; spores 1-celled, hyaline, navicular, 28–30 x 10–12 μ, with the contents slightly granular; paraphyses filiform, scarce.

The stromata are very characteristic; they are angular, dirty brown in color. The stromata are subepidermal and the row of epidermal cells is seen clearly above the clypeus. The spores are large, navicular. The species, which is apparently new, is referred to *Catacauma* on account of the position of the stromata in the leaf tissue.

On dead leaves of *Sabal* palm, Prov. Barahona, near sulphur springs beyond Duvergé, *Chardon 760*, July 11, 1937 (**type**).

Phyllachora Acaciae P. Henn., Hedwigia **33:** 233. 1894.

Widely distributed in tropical America on various leguminous trees and shrubs; stromata very minute, punctiform, less than 0.5 mm. in diameter, visible from both surfaces of the leaf, uniloculate; asci 60–70 x 20 μ (in our specimen); spores biseriate or inordinate, long-elliptical, 14–16 x 6–7 μ.

On *Acacia* sp., Prov. Duarte, road to San Francisco de Macoris, *Chardon & Toro 851*, July 11, 1937.

Phyllachora Bourreriae Stevens & Dalbey, Bot. Gaz. **68:** 54. 1919.

Our specimen has been compared with type material, which is *Stevens 4149*, from Vega Baja, Puerto Rico. Stromata amphigenous, black, circu-

lar, 1.0–1.5 mm. in diameter, enclosing many locules; spores obliquely uniseriate, elliptical, 8.5–12.5 x 7 μ.

On *Bourreria* sp., Prov. Puerto Plata, La Cumbre, Cordillera Septentrional, *Chardon 1129*, Aug. 30, 1937.

Phyllachora Exostemae Chardon sp. nov.

Stromata minuta, inconspicua, rotundata, 0.4–0.8 mm. diam., atra, in epiphyllo leniter arcuata, in hypophyllo vix visibilia, dispersa, non connata; loculi singuli, in mesophyllo centraliter insidentes, globosi vel fere globosi, 480–670 μ in diam., supra clypeo atro, crasso, loculum non superanti praediti, stromate incrassato, atro circumdati; asci longe cylindracei, octospori, 95–110 x 7–8 μ; sporae monostichae, continuae, hyalinae longe fusiformes, 12–14 x 4–5 μ; paraphyses praesentes.

Stromata minute, inconspicuous, circular, 0.4–0.8 mm. in diameter, black, slightly convex in the epiphyll, scarcely perceptible in the hypophyll, scattered, not coalescing; locule single, centrally located in the mesophyll, globose or approximately so, 480–670 μ in diameter, with a thick black clypeus above, not exceeding the locule, and heavy black stroma all around; asci long-cylindrical, 8-spored, 95–110 x 7–8 μ, with the spores uniseriate; spores 1-celled, hyaline, long-fusoid, 12–15 μ; paraphyses present.

On *Exostema* sp., Las Caobas, San José de Ocoa, *Chardon 781*, July 10, 1937 (**type**).

Phyllachora gratissima Rehm, Hedwigia **31:** 306. 1892.

The type is from Baños, Ecuador, collected by Lagerheim, in 1891. This is a well-known, conspicuous species, forming large, tar-like spots, 2–3 mm. in diameter, on the upper surface of the leaves of the avocado. It is common in the higher elevations in Puerto Rico and in the subtropical zone of the Andes of Venezuela and Colombia. The fungus seems to be restricted to the humid subtropical zones. Our collection from the Dominican Republic is not an exception to this rule.

On *Persea gratissima* L., Prov. La Vega, trail from Jarabacoa to Constanza, 600 m., *Chardon 1143*, Sept. 13, 1937; Constanza Valley, 1150 m., *Chardon 1170*, September 15, 1937.

Phyllachora insueta Sydow, Ann. Mycol. **23:** 372. 1925.

The species was originally described from material collected in Grecia, Costa Rica, on *Serjania caracasana* and distributed under Sydow's *Fungi exot. exs. 662*. Also known from various collections made by the writer in Venezuela and Colombia.

The stromata in the Dominican material are typical: pustule-like, raised above the leaf epidermis, yellowish-green, dotted with minute, black specks, which are the clypei of the locules. In cross section, the locules are numerous, labyrinthiform, with the leaf tissue hypertrophied around the locules. The spores are ellipsoidal, uniseriate, 15 x 6 μ. This is the first report of the fungus from the West Indies.

On *Serjania* sp., Prov. Samaná, Savanas, near Sabana la Mar, *Chardon 709*, July 5, 1937.

Phyllachora Masini Toro, Sci. Survey Porto Rico & Virgin Isl. **8** (1): 53. 1926.

The type specimen is from the mountains above Yauco, Puerto Rico, *Whetzel, Kern & Toro 2482*. The spots are black, circular, 1–2 mm. in diameter, more conspicuous in the epiphyll, bordered by a reddish zone of host tissue. The shape and measurement of the asci and spores agree with the type material.

On *Brunellia comocladifolia* H. & B., Prov. La Vega, trail from Constanza to Valle Nuevo, 1575 m., *Chardon 1181*, Sept. 16, 1937.

Phyllachora ocoensis Chardon sp. nov.

FIGURES 18–21

Stromata amphigena, parva, punctiformia, atra, rotundata, 0.5–1.0 mm. in diam., in hypophyllo convexa, in epiphyllo tantum leniter elevata; loculi singuli, globosi, 300–360 x 250–278 μ, ostiolo parvo epidermidem versus muniti, undique (praesertim infra supraque) membrana stromatica atra cincti; asci cylindrico-clavati, octospori, 95–110 x 17–19 μ; sporae distichae vel in asco aggregatae, continuae, hyalinae, longe naviculares, 17–23 x 4.5–6.0 μ, plasmate granuloso, homogeneo; paraphyses praesentes.

Stromata amphigenous, small, punctiform, black, circular, 0.5 to 1.0 mm. in diameter, convex in the hypophyll, only slightly raised in the epiphyll; locule single, globose, 300–360 x 250–278 μ, with a small beak facing the epidermis, surrounded on all sides (especially above and below) with black, stromatic tissue; asci cylindrical-clavate, 8-spored, 95–110 x 17–19 μ, with the spores biseriate or crowded in the ascus; spores 1-celled, hyaline, long-navicular, 17–23 x 4.5–6.0 μ, with the contents homogeneous; paraphyses present.

This small *Phyllachora* macroscopically resembles *Ph. Acaciae* P. Henn., a species of wide distribution in tropical America, but the stromata are more conspicuous. In *Ph. Acaciae* they do not reach 0.5 mm. in diameter. The spore characters are also different (in *Ph. Acaciae* they are 14–16 x 5 μ). A cross section of the leaf of our material shows that the base or bottom of the locule is in the hypophyll, where it bulges out conspicuously, while the upper portion of the locule has a small neck which faces the epiphyll.

On leguminous shrub (with pinnate leaves), Las Caobas, road to San José de Ocoa, *Chardon 773*, July 10, 1937 (**type**).

Phyllachora Ocoteicola Stevens & Dalbey, Bot. Gaz. **68:** 57. 1919.

Our material has been compared with the type specimen, *Stevens 4768*, from Monte Alegrillo, Puerto Rico. In the original diagnosis the spores are described as "oblong to cylindrical, 17–54 μ, somewhat pointed at one end." This is a gross typographical error. We have reexamined the type, as well as *Stevens 1520*, also from Puerto Rico, and they are 14–20 x 5–7 μ, with one end tapering.

In the specimen from the Dominican Republic, the stromata are black, shiny, angular, 2–3 mm. across, surrounded by a zone of dead host tissue, characters which compare well with the Puerto Rico material. The spores are 17–21 x 7–8 μ, a trifle larger, pointed at one end.

On *Ocotea* sp., Prov. La Vega, Constanza Valley, 1150 m., *Chardon 1175*, Sept. 14, 1937.

Phyllachora panamensis Stevens, Ill. Biol. Monogs. **11** (2): 37. 1927.

FIGURES 22–27

The type material is *Stevens 1351*, Fungi of Panama. Our Dominican material compares well with it in macroscopic characters, in the size and shape of the asci, and in the ellipsoidal spores 15–17 x 6–8 μ, which are arranged uniseriately in the ascus. It has also conidia which are small, globose to elliptical, about 2 μ long. Our specimen is not *Phyllachora Roureae* Sydow from the Philippines, the description of which was based on conidial material (Philippine Jour. Sci. **8** (4) sec. C: 227. 1923), distributed as *Sydow's Fungi exot. exs. 187*. We have examined this material and it has filiform conidia (stylospores) which measure 24–46 x 1–1.5 μ. (See fig. 26.)

On *Rourea glabra* H.B.K., Prov. La Vega, near Maimón, *Chardon 1064*, Aug. 13, 1937.

Phyllachora Phaseoli (P. Henn.) Theiss. & Sydow, Ann. Mycol. **13:** 507. 1915.

The type, *Physalospora Phaseoli* P. Henn. from Brazil, has not been examined, but our material has been compared with numerous specimens from Puerto Rico and with Sydow's *Fungi exot. exs. 667*, from San José, Costa Rica. The stromata are typical: punctiform, minute, in dense circular groups; the spores are 9–12 x 6–8 μ, broad-elliptical.

On *Phaseolus lunatus macrocarpus*, Hato del Yaque, *Ciferri 4842*, Feb. 7, 1932; on *Phaseolus* aff. *adenanthus*, road from Santiago to Puerto Plata, *Ciferri 4575*, Feb. 5, 1931; on *Phaseolus* sp., Dist. Nacional, ravine at Km. 30, Duarte Road, *Chardon 677*, June 30, 1939.

Phyllachora Scleriae Rehm, Hedwigia **39:** 232. 1900.

Originally described from South America. A common species in Puerto Rico, on *Scleria*; also known from Panama City (*Chardon & Nolla 188*). Spores long-fusiform, 19–21.5 x 5 μ. Probably present in other West Indian islands.

On *Scleria pterota* Presl., Prov. Trujillo, Sabana de Guabatico, north of Guerra, *Chardon 553*, June 20, 1937; Dist. Nacional, ravine at kilometer 30, Duarte Road, *Chardon 678*, June 30, 1937.

Phyllachora viequesensis Orton & Toro, Sci. Surv. Porto Rico & Virgin Isl. **8** (1): 54. 1926.

Stromata typical of the Phyllachoraceae on grasses and sedges, several loculate (mostly 2–3), the stromata formed in large air cavities beneath the epidermis of the host. Spores obliquely uniseriate, long-fusiform, 18–20 x 6 μ; paraphyses present. Our material has been compared with type material, *Whetzel, Kern & Toro 2648*, on the same host, from Vieques Island, Puerto Rico.

On *Cyperus ligularis* L., Prov. Samaná, beach at Sabana la Mar, *Chardon 688*, July 4, 1937; Prov. Barahona, shores of Lake Rincón, near Cabral, *Chardon 796*, July 11, 1937.

Phyllachora Paspalicola P. Henn., Hedwigia **48:** 106. 1908.

Common throughout tropical America, where the host plant is widely distributed. Spores lemon-shaped, 8–10 x 5–6 μ.

On *Paspalum conjugatum* Berg., Prov. Trujillo, San Cristobal, *Kern & Toro 156*, Mar. 12, 1926; Prov. Azua, Las Caobas, San José de Ocoa, *Chardon 779*, July 10, 1937; Puerto Plata, ravine at Km. 37, road to Puerto Plata, *Chardon 914*, Aug. 1, 1937; Prov. La Vega, ravine, base of Loma Peguera, *Chardon 1059*, Aug. 13, 1937.

Rhagadolobium cucurbitacearum (Rehm) Theiss. & Syd., Ann. Mycol. **12:** 275. 1914.

Spots conspicuous, in the undersurface of the leaf, appearing like dusted gunpowder. Reported from various Tropical American countries.

On *Gurania* sp., Prov. La Vega, trail from Jarabacoa to Constanza, 1100–1300 m., *Chardon 1145*, Sept. 14, 1937.

FIMETARIALES

Sordaria curvula De Bary, Morph. Phys. Pilze p. 209. 1866.

On cow dung, Prov. Azua, river forest, near San Juan de la Maguana, *Chardon 623*, June 27, 1937.

SPHAERIALES

Melanopsamma Milleri Chardon sp. nov.

FIGURES 5–8

Perithecia superficialia, atra, carbonacea, fere 0.8 mm. in diam., 0.1 mm. alta, hemisphaericalia usque conoidea, levia, non nitentia, Rosellinia similis, in strato ligneo subimmersa, ostiolo distincto papilliformi praedita; muro perithecii duplici, e pariete exteriore duro, carbonaceo, et interiore molli, brunneo composito; asci cylindracei, breviter pedicellati, maximi, 170–210 x 12–17 μ, apice et basi membrana tenui pseudoparenchymatica e paraphysoideis composita tunicati, octospori; sporae ex parte distichae in asco dense compressae, uniseptatae, hyalinae, longe fusiformes, interdum subarcuatae, ad septum constrictae, magnae, 59–64 x 9–12 μ, leves, utrinque acutae; paraphysoidea filiformia.

Perithecia superficial, black, carbonaceous, about 0.8 mm. in diameter, 1.0 mm. in height, hemispherical to conical, with the surface smooth, not shiny (*Rosellinia*-like), seated on the woody substratum where they are slightly immersed, and provided with a pronounced papilliform ostiolum; perithecial wall made up of a double wall, the outer hard, carbonaceous, and the inner brown and soft; asci cylindrical, short-pedicellate, very large, 170–210 x 12–17 μ, embedded in paraphysoids that are connected with a fine pseudoparenchymatous tissue on the top of the perithecium and a similar one at the base, 8-spored, with the spores partially biseriate, closely pressed in the ascus; spores 1-septate, hyaline, long fusiform, sometimes slightly arcuate, constricted at the septum, large, 59–64 x 9–12 μ, smooth, with the ends acute; paraphysoids filiform.

A beautiful species, picked up for a *Rosellinia*. The conspicuous black perithecia are seated on the woody matrix with no subiculum or stroma. The species is dedicated to Dr. Julian H. Miller, of the University of Georgia, a distinguished student of the Sphaeriales, who confirmed the determination of the fungus as a new species and its inclusion under *Melanopsamma*.

On dead wood, La Vega, forests at El Hatillo, near Yuna river, *Chardon 1094*, Aug. 28, 1937 **(type)**.

Lasiosphaeria pezizula (Berk. & Curt.) Sacc. Syll. Fung. **2:** 195. 1883.
Sphaeria pezizula Berk. & Curt., Grevillea **4:** 106. 1875.

Previously known from Puerto Rico, Bermuda, and continental North America. (Determination made by Professor H. M. Fitzpatrick.)

On dead wood, La Vega, near Jarabacoa, *Chardon 1229*, Sept. 13, 1937.

Calyculosphaeria calyculus (Mont.) Fitzpatrick, Mycologia **15:** 51. 1923.
Sphaeria (*Caespitosa*) *calyculus* Mont., Ann. Sci. Nat. ser. II, **14:** 322. 1840.
Sphaeria calyculus Mont., Syll. Crypt. p. 226. 1856.

For more details of this interesting species see Fitzpatrick (*l.c.*). The type is from French Guiana, collected by Leprieur. (Determined by Dr. J. H. Miller.)

On decaying fence posts, La Vega, Maimón River, near Maimón, *Chardon 1009*, Aug. 13, 1937.

Leptosphaeria Cecropiae Chardon sp. nov.

Maculae amphigenae, epiphyllae parvae, rotundae, 1.0–1.5 cm. in diam., centro peritheciis aggregatis atratae, hypophyllae pustulatae, parvae, argenteae ut colore folii, ostiolis peritheciorum minute punctulatae; perithecia pluria, 5–12, in quaque macula, lageniformia, 240–300 x 215–270 μ, pariete brunnea praedita; asci cylindracei, 175–190 x 12–14 μ, octospori; sporae oblique monostichae, longe fusoideae, clare brunneae, 3-septatae, ad septa constrictae, una cellula terminali attenuata; paraphyses filiformes, numerosissimae.

Spots amphigenous, in the epiphyll appearing as small, circular, brown spots, 1–1.5 cms. in diameter, with the center black due to the coalescing perithecia; in the hypophyll pustule-like, small, of the same silver color as the leaf, but showing minute black spots which are the necks of the perithecia; perithecia several (5–12) on each spot, flask-like in section, 240–300 x 215–270 μ, provided with a brown wall; asci cylindrical, 175–190 x 10–14 μ, 8-spored, with the spores obliquely uniseriate in the ascus; spores long-fusoid, distinctly brown, 3-septate, constricted at the septa and one end cell tapering; paraphyses filiform, very abundant.

Macroscopically, the pustule-like spots which appear on the undersurface of the leaf are typical. Both the asci and spores show beautifully under the microscope.

On *Cecropia peltata* L., Kilometer 67, near La Cumbre, road to Bonao, *Chardon & Toro 832*, July 11, 1937 (**type**).

Leptosphaeria Smilacis Chardon sp. nov.

Maculae magnae, in utraque pagina folii visibiles, conspicuae, orbiculares vel ellipticae, plus minus 1.0 cm. in diam., vel confluentes et majores, subalbae, peritheciis numerosis minutis punctatae, e zona atra definita marginatae; perithecia minuta, in textura matricis immersa, globosa, 145–170 μ in diam., pariete definito e cellulis brunneis composito, non-ostiolata; asci cylindrico-clavati, octospori, parvi, 47–55 x 8–9 μ, in stipitem brevissimum contracti; sporae irregulariter conglobatae, brunneae, 3-septatae, longe fusiformes, subcurvatae, 14–19 x 4–5 μ; paraphyses praesentes.

Spots large, visible on both surfaces of the leaves of the host, conspicuous, circular, or elliptical, about 1 cm. in diameter or larger through coalescence, whitish, with numerous minute specks (perithecia) in the

spot, provided with a definite blackish margin; perithecia small, immersed in the host tissues, globose, 145–170 μ in diameter, with a definite cell wall made up of brown cells, without a beak; asci cylindrical-clavate, 8-spored, small 47–55 x 8–9 μ, short-stipitate, with the spores inordinately pressed together; spores brown, 3-septate, long-fusiform, slightly curved, 14–19 x 4–5 μ; paraphyses present.

The spots produced by this fungus are very conspicuous on both surfaces of the leaves of the host, with many minute specks and a definite border. The asci are clearly seen under the microscope with the brown, 3-septate spores tightly pressed together.

On *Smilax* sp., Distrito Nacional, road from Ciudad Trujillo to Bocachica, *Chardon 539*, June 13, 1937 (**type**).

Didymosphaeria Trichostigmae Chardon sp. nov.

Maculae amphigenae, brunneae, fere orbiculares, 2–4 mm. in diam., margine indefinita cinctate; perithecia in maculis densiuscule (6–13) disposita, semper epiphylla, inconspicua, punctiformia, globosa, parva, 210–280 x 160–175 μ, pariete cellulari definito, circa ostiolum incrassato et obscuriore praedita; asci numerosi, fasciculati, cylindracei, octospori, 95–133 x 8–10 μ; sporae inordinatae, bicellulares, elongatae, brunneae, ad septa constrictae, 28–34 x 3–4 μ; paraphyses praesentes.

Spots amphigenous, light brown, approximately circular, 2–4 mm. in diameter, with the margins indefinite; perithecia crowded in the spots (6–15 in number), visible only in the epiphyll, inconspicuous, punctiform, globose, small, 210–280 x 160–175 μ, provided with a definite, brown, cellular perithecial wall, which thickens around the region of the ostiolum and becomes dark brown, the numerous asci fasciculate inside the perithecium; asci cylindrical, 8-spored, 95–135 x 8–10 μ, with the spores inordinate; spores 2-celled, long rod-like, brown, constricted at the septum, 28–34 x 3–4 μ; paraphyses present.

This is different from *Linospora Trichostigmae* Stevens, described on the same host from Puerto Rico. In Clements and Shear (3, p. 68), there are two genera in the Sphaeriaceae-Phaeodidymae which have close perithecial characters: *Stegastroma*, with a clypeus, and *Didymosphaeria* without a clypeus. Our specimen has no clypeus; the brown tissue occurring around the region of the ostiolum is produced by a thickening of the perithecial wall. Although the walls of this perithecial neck attains a thickness of 50–60 μ, it neither loses its cellular structure, nor becomes black, and hence cannot be interpreted as a clypeus. The asci inside the perithecia are basal-peripheral which fits with *Didymosphaeria*.

On *Trichostigma octandrum* (L.) H. Walt., Duarte, road to San Francisco de Macoris, *Chardon & Toro 853*, July 11, 1937 (**type**).

Metasphaeria phyllachoracearum Petrak, Ann. Mycol. **29:** 350. 1931.

Telimena domingensis Chardon, Jour. Dept. Agric. Porto Rico **13:** 14. 1929.

The specimen cited below, *Kern & Toro 156*, was studied by the writer in 1929 (*l.c.*) and described as a new species of *Telimena*, on the basis of the spores being "fusoid, 3-septate, hyaline to greenish, with both ends acute, 12–14 x 2–3 μ."

The researches of Dr. F. Petrak (Mykologische Notizen, XI, *l.c.*) have thrown new light on this fungus. He did not see the type material, but from examination of other material made available to him by Dr. R. Ciferri, he concluded there was no *Telimena*, and that the asci and 3-septate, hyaline, fusoid spores were the ascosporic stage of a *Metasphaeria* parasitic on the stromata of certain Phyllachoraceae. A reexamination of the type of *Telimena domingensis* Chardon has convinced the writer that he was in error, and that Petrak's interpretation is the correct one.

On old phyllachoroid stromata on *Paspalum conjugatum* Berg., San Cristobal, *Kern & Toro 156*, March 12, 1926.

Pleospora Doidgeae Petrak, Ann. Mycol. **25:** 295. 1927.

Dictyochorella Andropogonis Doidge, Bothalia **1:** 66. 1921.

The synonymy of these two species was clearly established by Petrak (*l.c.*). The type of Miss Doidge's species is on *Andropogon nardus* from Natal, South Africa. The species was found in Venezuela by the writer, parasitic on various phyllachoroid stromata, and careful drawings were made. (See Monogr. Univ. Puerto Rico, Ser. B, No. **2**, *plate XXXI, figs. 2–3*, 1934.)

In the material from the Dominican Republic the perithecia are found inside or adjacent to old phyllachoroid stromata; they are clearly provided with a brown, cellular, perithecial wall; asci 65–85 x 8–10 μ, 8-spored, with the spores inordinate; spores muriform, brown, with one of the central cells longitudinally septate, 17–19 x 5–6 μ. This leaves no doubt as to the identity of the species, which is the first record of its occurrence in the West Indies.

On old phyllachoroid stromata, on *Andropogon bicornis* L., Distrito Nacional, ravine al Kilometer 30, along Duarte Road, *Chardon 672*, June 30, 1937.

FUNGI IMPERFECTI

Phyllosticta Citharexyli Chardon sp. nov.

Maculae amphigenae, conspicuae, fere orbiculares vel irregulares, 4–7 mm. in diam., zona decolorata membranae matrici emortuae, e pycnidiis numerosis atris punctata compositae, margine definita, conspicua, leniter elevata rubro-violacea circumdatae; pycnidia globosa vel subglobosa, in membrana folii epiphyllum versus immersa, parva, 93–120 x 72–81 μ, cellulis definitis composita; conidia unicellularia, hyalina, ovata, 8–9 x 5–7 μ.

Spots amphigenous, conspicuous, approximately circular or irregular in outline, 4–7 mm. in diameter, made up of a discolored zone of dead host tissue in which may be seen numerous small, black specks (the pycnidia), the dead tissue being surrounded by a definite, conspicuous, slightly raised margin of reddish violet tissue; pycnidia globose or nearly so, immersed in the tissues of the leaf, facing the epiphyll, small, 93–120 x 72–81 μ, made up of distinct wall cells; conidia 1-celled, hyaline, ovate in shape, 8–9 x 5–7 μ.

On *Citharexylon* sp., Prov. Samaná, *Chardon 744*, July 6, 1937 (**type**); Prov. Santiago, San José de las Matas, *Chardon 483*, June 6, 1937.

Phyllosticta Stigmatophylli Chardon sp. nov.

Maculae fere orbiculares vel irregulares, amphigenae, 2–4 mm. in diam., epiphyllae subalbae, centro pycnidiis numerosis laxe dispersis punctatae, linea definita, parum elevata cincta, hypophylla sordide brunneae, sine linea definita; pycnidia dispersa, immersa, globosa, 110–125 μ in diam., non-ostiolata, semper epiphylla; conidia hyalina, unicellularia, ovoidea usque ellipsoidea, 7–9 x 5–6 μ, numerosissima.

Spots nearly circular or irregular in outline, amphigenous, 2–4 mm. across, whitish in the epiphyll, with numerous specks (pycnidia) scattered in the center of the spot, with a slightly elevated, definite black margin which makes the spot conspicuous; in the hypophyll the spots are dirty black in color, without a pronounced border; pycnidia scattered over the infected spot, immersed globose, 110–125 μ in diameter, not beaked, restricted to the upper side of the leaf; conidia hyaline, 1-celled, ovoid to ellipsoidal, 7–9 x 5–6 μ, very numerous.

On *Stigmatophyllon* sp., Prov. Santiago, San José de las Matas, *Chardon 494*, June 6, 1937 (**type**).

Cylindrosporium Securidacae Chardon sp. nov.

Maculae amphigenae, angulares, parvae, 1.0–1.5 mm. in diam., centro brunneae, margine obscuriore, parum elevato cinctae; acervuli subepidermicales, 100–120 μ in diam.; conidia unicellularia, hyalina, longe bacillaria, arcuata, 17–25 x 3 μ, plasmate homogeneo, in conidiophoris hyalinis acutis oriunda.

Spots amphigenous, angular, small, 1.0–1.5 mm. across, brown in the center, with a slightly raised dark margin; acervuli subepidermal, 100–120 μ across; conidia 1-celled, hyaline, long rod-like, curved, 17–25 x 3 μ, with the contents homogeneous, borne on hyaline tip-like conidiophores.

On *Securidaca volubilis*, Prov. Samaná, beach at Sabana la Mar, *Chardon 695*, July 4, 1937 (**type**).

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EXPLANATION OF FIGURES

Figs. 1–4. *Nymanomyces Xolismae* sp. nov.

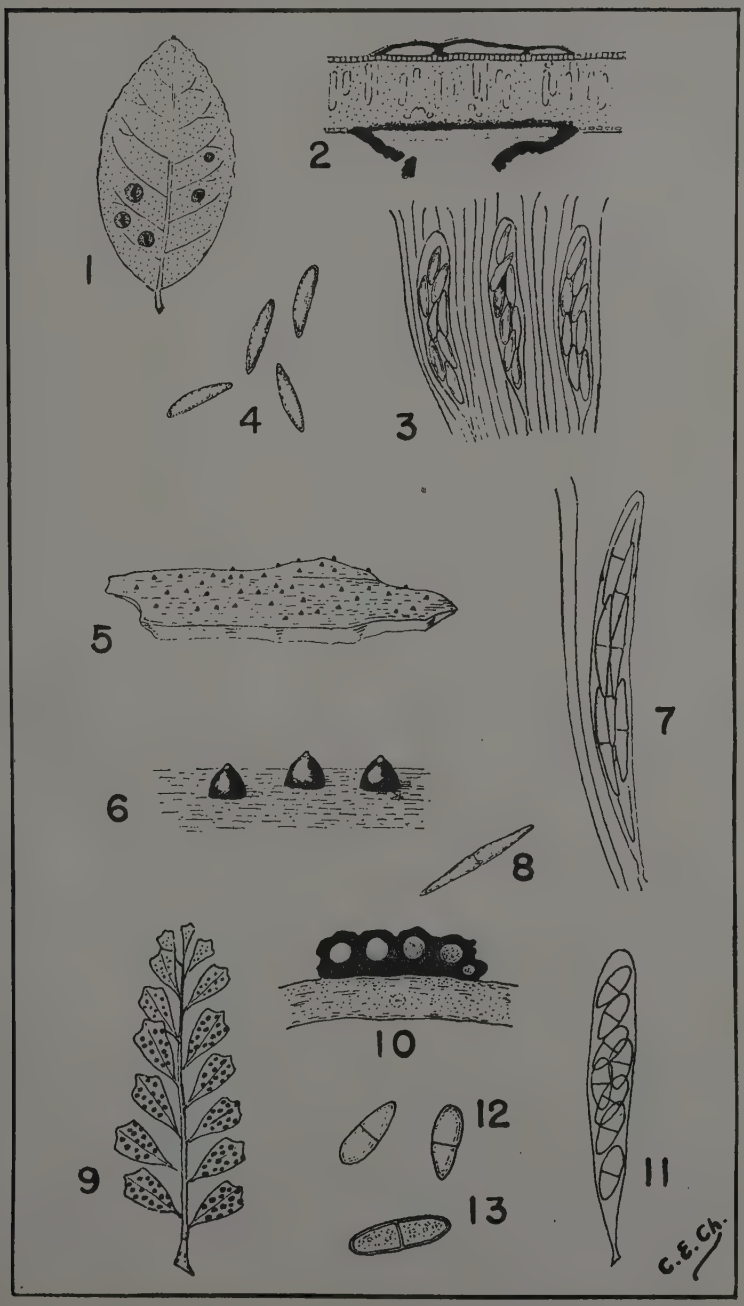
1. Leaf of *Xolisma* sp. showing hypophyllous ascoma opening by a longitudinal slit.
2. Cross section of leaf of ruptured ascomata in the hypophyll disclosing the hymenium and epiphyllous sterile stromata.
3. Portion of the hymenium with asci and numerous paraphyses.
4. Individual ascospores.

Figs. 5–8. *Melanopsamma Milleri* sp. nov.

5. Perithecia, natural size.
6. Perithecia under binocular, showing papilliform ostiolum; seated and partially immersed in the woody matrix.
7. An ascus and two paraphyses.
8. Ascospore.

Figs. 9–13. *Dothidella domingensis* sp. nov.

9. Habitat sketch of fungus on leaves of *Baccharis myrsinites*.
10. Cross section of leaf showing position of compound stroma with several locules.
11. Ascus and spores.
12. Individual ascospores, showing septation, with one cell larger and obtuse, and the other cell smaller, with a subacute end (note that there is no thickening of the cell wall).
13. Individual ascospores of *Dothidella tinctoria* showing differences from the above (note the larger size, the ascospore divided into two cells of approximately the same size, and the thick cell wall).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Figs. 14–17. *Catacauma Sabal* sp. nov.

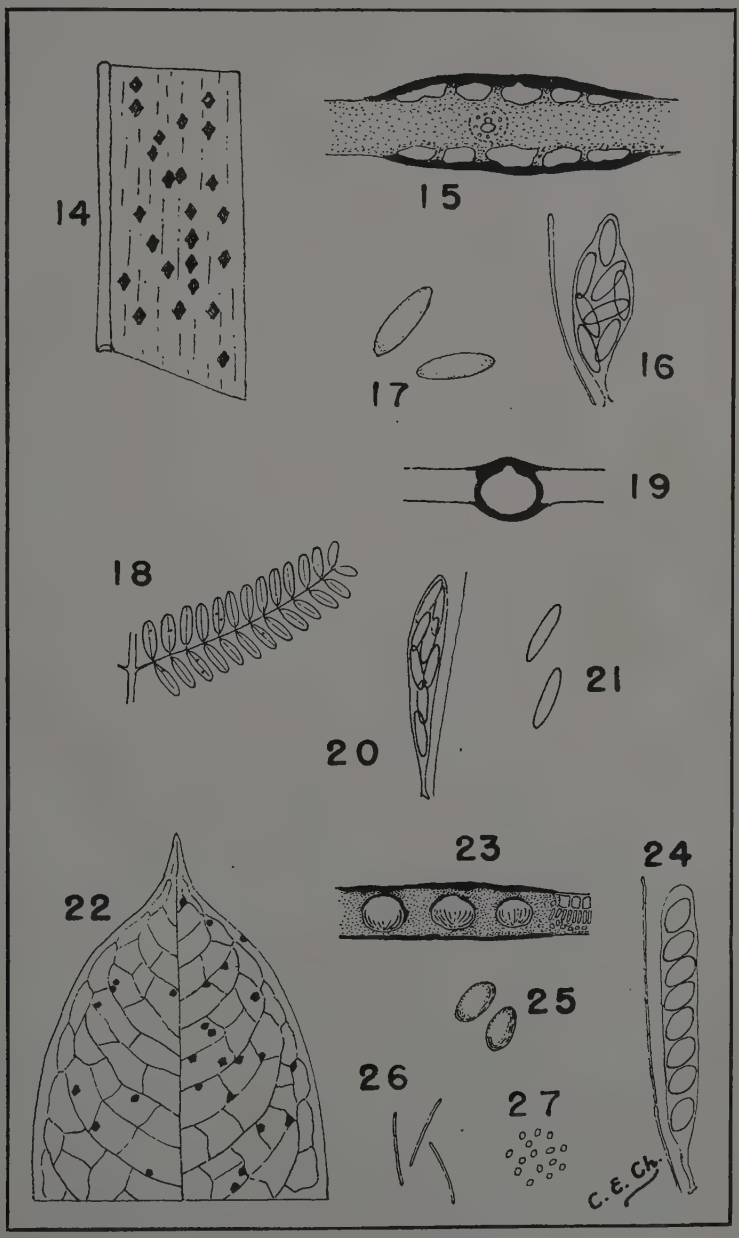
14. Habit sketch of fungus on a portion of a leaf of *Sabal* sp.
15. Cross section of leaf showing amphigenous, loculate, angular stromata located between the epidermis and the mesophyll.
16. Clavate ascus and paraphyses with ascospores inordinately pressed in the ascus.
17. Two ascospores.

Figs. 18–21. *Phyllachora ocoensis* sp. nov.

18. Habit sketch of pinnate leaves, leguminous shrub with small punctiform stromata.
19. Cross section of a pinna of the same with uniloculate stroma in the mesophyll.
20. Ascus and thread-like paraphyses.
21. Two individual ascospores.

Figs. 22–27. *Phyllachora panamensis* Stevens.

22. Habit sketch of fungus on leaves of *Rourea glabra*, showing angular stromata.
23. Cross section of leaf showing position of stromata and locules in the mesophyll.
24. Ascus and paraphyses.
25. Two individual ascospores.
26. Stylospores (*Phyllachora Roureae*).
27. Conidia (*Ph. panamensis*).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2(4):475–525 FARLOWIA JULY, 1946

THE BIOLOGY OF GYMNOSPORANGIUM NIDUS-AVIS THAXTER

ALTON E. PRINCE [1]

HISTORICAL RÉSUMÉ

The history of our knowledge of *Gymnosporangium nidus-avis* Thaxter is varied and interesting. This has resulted from several circumstances. (1) The rust has proved to be heteroecious, and we now know that it affects many host species in both its aecial and telial phases. (2) The elucidation of its hosts has proceeded slowly, at times uncertainly. (3) The manifestations of the hosts carrying the telial phase are confusing, for while usually they are witches' brooms with juvenile, subulate leaves, in other instances they are brooms with adult, scale-shaped leaves, and in still others they are slight fusiform stem swellings or only simple twig, branch or stem infections. A still further complication is now added as a result of studies recorded in this paper which presents evidence that the heretofore recognized *G. juvenescens* Kern is not distinguishable from *G. nidus-avis*.

The history begins with two collections made by Ravenel along the Santee Canal, South Carolina, in the spring seasons of 1848 and 1850 respectively. These specimens are now a part of the Curtis collection in the Farlow Herbarium, and bear the original labels under the designation *Gymnosporangium Juniperi* Lk. About thirty years later Farlow (1880) called attention to them and decided that they were properly *G. conicum* DC.[2] Since Ravenel's time many collections of *G. nidus-avis* have been made and there are scores of references to this species in the literature, but the latter are of interest mainly from the standpoint of geographical distribution. This resumé, however, will be restricted to a brief survey of the taxonomic and biological contributions pertinent to the author's studies. Thus it includes only references to the works of Farlow, Thaxter, Arthur, Kern, and the few others who have made additions of some significance. In this connection, Farlow and Thaxter stand out as the pioneer contributors.

Farlow (1880) was actually the first to give a description of *G. nidus-avis*. This he did in his notable monograph on the Gymnosporangia of the United States. He described it as an American representative of the European *G. conicum* DC. on *Juniperus virginiana*, but he included specimens of this rust characterized only by fusiform stem swellings and pul-

[1] Thesis submitted in partial fulfillment of the requirements for the Degree of Doctor of Philosophy at Harvard University.

[2] The *G. conicum* DC referred to by Farlow (1880, pp. 23–24) is in my judgment what is now known as *G. juniperinum* (L.) Mart.

vinate telia. In the same paper he made mention of rust brooms on *Juniperus virginiana*, but ascribed them to *G. clavipes* C. & P. The illustrations in his monograph (1880, *Pl. 2, figs. 22–27*), however, represent perfectly what Thaxter subsequently described under the name *G. nidus-avis*.

In a second paper, Farlow (1886a) stated that the broom rust on red cedar previously referred to by him as *G. clavipes* likewise produces its *Roestelia* on *Amelanchier*. The same year Farlow (1886b) confirmed the previous report that his *G. conicum* was the cause of brooms on *Juniperus virginiana*, although his cultures failed to produce aecia on *Sorbus* (one of the known hosts of *G. conicum* in Europe). In spite of this failure he was unshaken in his conviction that the rust was *G. conicum*, and he expressed the belief that additional cultures would demonstrate *Sorbus* to be a host. If this had been proven then to be the case, Thaxter probably would not have continued investigations which later led to the establishment of a new species.

The work of Thaxter is fundamentally significant because of its biological findings. He reported (1887) inoculations of Farlow's *G. conicum* on *Amelanchier canadensis*,[3] *Aronia arbutifolia*, *Sorbus americana* (*Pyrus americana*) and *Malus pumila* (*Pyrus Malus*). The *Amelanchier* only became infected, and on it were produced both spermogonia and aecia. As an indication of the extreme variability exhibited by this species, he noted that he was unable to distinguish the aecia from those of his *Roestelia lacerata y* (*G. globosum* Farl.) even though the former matured two months earlier than the latter. Thaxter (1889) reported two further series of cultures. In the first, inoculations were made on *Amelanchier canadensis*, *Crataegus coccinea*, *Malus pumila* (*Pyrus Malus*), and *Sorbus*. Again, only the *Amelanchier* became infected and, as before, both spermogonia and aecia were produced. The second series was restricted to cultures made on *Amelanchier*. Following these experiments he stated that the result was "similar in all respects to that obtained in previous years." From these investigations he reached the following significant conclusions: "In relation to our 'birds' nest' *Gymnosporangium*, the question of identities is still further confused by my cultures of this species, made during three successive years with identical results. The *Roestelia* obtained . . . was referred to *R. cornuta*, there being no other alternative among described American Roestelias. . . . It should be noted that upon *Sorbus* the 'birds' nest' *Gymnosporangium* has given no result whatever. Further careful cultures and observation together with a more extended examination of European specimens than I have been able to make, will of course be necessary to confirm this supposition; but I am decidedly of the opinion that our 'birds' nest' species is a distinctly American form as yet unnamed."

[3] The name *Amelanchier canadensis* should now be referred to *A. arborea* (Michx. f.) Fernald, and the name *A. oblongifolia*, in part, to *A. canadensis* (L.) Medic. Rhodora **43**: 559–567. 1941.

Two years later Thaxter (1891) published a description of the telial and aecial stages of the new species under the name *G. nidus-avis*. He also republished these descriptions in 1892 and 1893. Specimens of Thaxter's cultures of *G. nidus-avis* are in the Farlow Herbarium and have been carefully examined by me. The groundwork being thus firmly laid, it remained for others to confirm and extend it.

During the period between 1908 and 1915, Arthur (1908) reported inoculations on *Amelanchier intermedia*, and *Malus pumila* var. *Whitney Crab* (*Malus Malus* var. *Whitney Crab*). The apple plant only became infected. This produced both spermogonia and aecia on its leaves. In 1910 he reported on additional cultures made in 1909, when *Amelanchier canadensis*, *Crataegus Pringlei*, and *Malus ioensis* were inoculated. The *Malus* and *Crataegus* became infected, the former producing spermogonia and aecia, the latter spermogonia only. The *Amelanchier* remained uninfected. In his report of cultures made in 1910, he stated that the fruit of *Amelanchier ovalis* (*A. vulgaris*) and the leaves of *Cydonia oblonga* (*C. vulgaris*) and *Malus coronaria* were inoculated but only the *Amelanchier* became infected, and it produced spermogonia and aecia. A second series of inoculations was made later in the same year on identical specific hosts. That time the *Malus* alone became infected, but with the production of spermogonia only; the leaves died before aecia could be developed. Finally Arthur (1915) reported his last cultures of this rust. *Amelanchier ovalis* (*A. vulgaris*) was inoculated and both spermogonia and aecia were produced. Arthur (1934) in summary has recently listed the following names of plants that serve as hosts of *G. nidus-avis*: for the aecial stage — *Amelanchier canadensis*, *A. erecta*, *A. intermedia*, *A. laevis*, *A. oblongifolia*, *A. ovalis* (*A. vulgaris*), *Crataegus Pringlei*, *Cydonia oblonga* (*C. vulgaris*), *Malus pumila* (*Malus Malus*); for the telial stage — *Juniperus virginiana*.

Dodge was the next important contributor. His most notable work concerned teliospore formation and production, and this will be reviewed in the section below dealing with life history of the fungus. He also (1918b, pp. 294–295) published the results of cultures of *G. nidus-avis* made between 1914 and 1917. A species each of *Amelanchier* and *Malus* was inoculated in the spring of 1914 with inoculum from telia borne in the axils of leaves on brooms, from the stems of brooms, and from sori on the tree trunk. Some aeciospores from these cultures were used to inoculate a potted red cedar plant in June 1914. No external symptoms of infection appeared in 1915. Two small sori became evident in May 1916. By 1917 these two sori had coalesced and produced a telial mass two inches long. This infection spread vertically five inches in three years. On May 10, 1916 telia were collected in the field for inoculation purposes. The sowings were made on *Amelanchier* "*canadensis*," May 17, and aecia were produced June 17. A cedar was inoculated with spores from this culture on June 21. On March 22, 1917, twenty-one days after being taken from a cold frame, a telium appeared in the axil of one leaf. The

next year, on February 19, 1918, two more sori appeared. Thus under favorable conditions telia may be produced the spring following inoculation. Dodge (1918c) thus found that telial sori of *G. nidus-avis* sometimes develop "on the blades of leaves." Dodge (1931) found that *G. nidus-avis* was very destructive to eastern red cedar trees. As emphasized by him, this is very much in contrast to the general belief that it is only the aecial host which is injured. According to him (1934) the common red cedar is subject to attacks by *G. nidus-avis* of such severity as to cause the premature death of the suscept.

As a matter of minor interest, reference may properly be made to Clinton and McCormick's (1924) Petri-dish cultures of *G. nidus-avis*. Leaves of *Cydonia oblonga* (*C. vulgaris*), *Malus ioensis* (*Pyrus ioensis*), *Malus pumila* (*Malus communis*), and *Malus pumila* var. *Wealthy* (*Pyrus Malus* var. *Wealthy*) were placed on a liquid medium in Petri-dishes and inoculated with basidiospores of the fungus. Spermogonia developed on the apple and quince leaves; aecia did not develop because of the unfavorable method of culture. The other inoculations gave negative results.

Prince and Steinmetz (1940) were the next to investigate *G. nidus-avis* when cultures of 1936 and 1937 were reported. In 1936, they inoculated *Amelanchier canadensis*, *A. laevis*, *A. stolonifera*, *A. canadensis* × *A. stolonifera*, *Malus pumila* var. *Wealthy* (*M.* sp. var. *Wealthy*); all except the apple became infected and produced spermogonia and aecia. In 1937 the plants inoculated were *Amelanchier canadensis*, *A. laevis*, *A. stolonifera*, *A. Wiegandii*, *A. canadensis* × *A. stolonifera*, *Cydonia oblonga* (*C. vulgaris*), *Chaenomeles japonica* (*Cydonia japonica*), *Malus* sp. and *Sorbus americana*; all of these except the *Chaenomeles*, *Malus* and *Sorbus* produced spermogonia and aecia. In addition to their culture experiments they made careful taxonomic comparison of the broom-forming rust of *G. juvenescens* on *Juniperus horizontalis*, with *G. nidus-avis* on *Juniperus virginiana*, making use of their cultures, field collections, and specimens obtained from various herbaria. No differences could be found in the spermogonial, aecial or telial stages of these rusts. Hence the morphological evidence clearly indicated that *G. juvenescens* differed in no respect from *G. nidus-avis*. But culture work was necessary before a final conclusion could be drawn. Should culture experiments confirm the tentative taxonomic conclusions of Prince and Steinmetz, the addition of *Juniperus horizontalis* as a telial host of *G. nidus-avis* is of greater significance than just the addition of another name to a host list. This is important because this telial host extends from the Atlantic nearly to the Pacific coast (see map p. 483) and this is a connecting link between the eastern and western red cedars, *Juniperus virginiana* and *J. scopulorum* respectively, (the latter being another recognized telial host of the so-called *G. juvenescens*).

The history of what, up until the present work, has been called *Gymnosporangium juvenescens* Kern will now be added to that of *G. nidus-avis*. Arthur (1907) reported the first cultures of the western rust, which at that time was determined as *G. Nelsoni* Arth. Telia from *Juniperus scopulorum*

were used as a source of inoculum for cultures which yielded spermogonia on *Amelanchier canadensis* and *Sorbus americana* but no aecia were formed. *Crataegus Pringlei, Chaenomeles japonica* (*Pyrus japonica*), and *Aronia melanocarpa* (*Aronia nigra*) were inoculated but no infection occurred. Arthur (1908) reported two series of cultures of "*G. Nelsoni*" later recognized by him to be *G. juvenescens*, using inoculum from *J. scopulorum*. In the first series, *Amelanchier intermedia* was inoculated and spermogonia appeared, but because of injury to the plant no further development took place. The second series was started about two weeks later using inoculum from a second collection of telia on *J. scopulorum*. Sowings were made on two plants of *Amelanchier canadensis* upon which were produced both spermogonia and aecia.

In regard to these cultures Arthur (1908) made the following statement: "The above results confirm and much extend the somewhat uncertain work of last season. It leaves no further doubt that *Roestelia Nelsoni* Arth. should be counted as a synonym of *G. Nelsoni* Arth. as suggested in the original publication of the name." This statement shows, more than anything else, the difficulty early investigators had in definitely placing the extremely variable species under consideration, since *G. Nelsoni* today is a valid species.

Arthur (1909) reported additional cultures of his "*G. Nelsoni*" using inoculum from the usual source. *Amelanchier erecta* and *Sorbus americana* were inoculated and spermogonia were produced on both hosts, but aecia only on the *Sorbus*. Arthur (1912a) reported the last cultures of this "*G. Nelsoni*" which were conducted during the spring of 1910. The inoculum used was obtained from *Juniperus virginiana*, and *Amelanchier erecta, Cydonia oblonga* (*C. vulgaris*) and *Malus coronaria* were inoculated. *Amelanchier* was the only host successfully infected and on it were produced spermogonia and aecia. Arthur (1912b) called attention to the fact that previous cultures reported under *G. Nelsoni* should be referred to *G. juvenescens* Kern.

Kern (1911) described the aecial and telial stages of a broom-forming rust on *Juniperus scopulorum* and *J. virginiana* under the name of *G. juvenescens*. As aecial hosts he cites *Amelanchier alnifolia, A. florida, A. oreophila, A. polycarpa*, and *A. pumila*. The distribution of the new species is given as "British Columbia and Alberta southeast to the Black Hills of South Dakota and to Colorado, and locally in Nebraska and Wisconsin."

Arthur (1934) subsequently gave a similar description and range of *G. juvenescens*. A number of hosts were added. For the spermogonial and aecial phases are given *Amelanchier alnifolia, A. Bakeri, A. canadensis, A. florida, A. humilis, A. Jonesiana, A. mormonica, A. oreophila, A. polycarpa, A. pumila, A. spicata* and *Sorbus americana*; as telial hosts *Juniperus horizontalis, J. scopulorum* and *J. virginiana*.

According to hitherto apparently unpublished data found on specimens and in letters now in the Farlow Herbarium, the late Dr. J. J. Davis likewise carried out cultures with *G. juvenescens* in 1918. It was he who

first recognized that brooms on *Juniperus horizontalis* were the result of a rust infection. Using inoculum from this source, sowings were made on *Amelanchier oblongifolia* on which both spermogonia and aecia were produced.

Fraser (1925) inoculated *Amelanchier alnifolia* with spores of *G. juvenescens* collected on *Juniperus horizontalis*. Spermogonia and aecia developed.

During the spring of 1935, Steinmetz and Hilborn (Prince and Steinmetz, 1940) using inoculum from *J. horizontalis*, which had previously been determined as *G. juvenescens* by Dr. J. C. Arthur, inoculated an undetermined species of *Amelanchier* which resulted in the production of spermogonia and aecia. They were unable to differentiate what was supposed to be *G. juvenescens* by cultures from *G. nidus-avis* made on the same *Amelanchier* plant. Prince and Steinmetz (1940) reported cultures made in 1936 and 1937 with inoculum from *Juniperus horizontalis* on *Amelanchier canadensis*, *A. canadensis* × *A. stolonifera*, *A. laevis*, *A. stolonifera*, *A. Wiegandii*, *Chaenomeles japonica* (*Cydonia japonica*), and *Cydonia oblonga* (*C. vulgaris*). Spermogonia and aecia were produced on all of these hosts except *Chaenomeles japonica*. The aecia produced were in all respects the same as those produced in parallel cultures of *G. nidus-avis*. It should be noted that the *Cydonia* was successfully inoculated because this host genus was not known previously as a host for *G. juvenescens* but was for *G. nidus-avis* and had served until then as one of the reasons which justified separating *G. juvenescens* from *G. nidus-avis*.

In consideration of the conflicting evidence presented by previous investigators, it has seemed desirable not only to study further the life histories of *G. nidus-avis* and the fungus called *G. juvenescens*, but also to make additional extensive inoculations in order to verify and add to, as far as possible, the work of these investigators. Thus the present studies were carried out with the hope of adding to the knowledge of the life history of the organism.

TAXONOMY

The nomenclature of *Gymnosporangium nidus-avis* Thaxter is probably less complicated than any other of the widely distributed North American species belonging to this genus. This is certainly not because of the uniformity of symptoms produced by the fungus since no species of *Gymnosporangium* other than *G. nidus-avis* causes more than one distinct type of fasciation of its telial host and in addition produces a variety of symptoms on the branches and stems. In the aecial phase it is very similar to several species occurring on the same aecial hosts, an example of which was given by Thaxter (1889), when he pointed out the uncertainty of distinguishing *G. nidus-avis* and *G. clavariaeforme* by gross appearance alone. This and other similarities are in part the cause of the not infrequent mislabeling of collections found in herbaria. Therefore it can

be said that the present simplicity in the nomenclature of this species is undoubtedly because of the thoroughness with which it was studied prior to its publication by Thaxter, and to the completeness and accuracy of his first description (1891). The following binomials have been applied to the rust now known as *Gymnosporangium nidus-avis* Thaxter. The phase in the life cycle to which the name was affixed is indicated by the Roman numeral at the left.

III **Gymnosporangium nidus-avis** Thaxter, Bull. Conn. Agr. Exp. Sta. **107:** 6. 1891.

III *G. clavipes* C. & P. *sensu* Farlow, Anniv. Mem. Bost. Soc. Nat. Hist. pp. 21–22. pl. 2, figs. 22–27. 1880.

III *G. conicum* Hedw. f. in DC. Flora Franc. *sensu* Farlow, Anniv. Mem. Bost. Soc. Nat. Hist. pp. 23–24. 1880.

O, I *Roestelia nidus-avis* Thaxter, Bull. Conn. Agr. Exp. Sta. **107:** 6. 1891.

III *Puccinia nidus-avis* (Thaxt.) O. Kuntze, Rev. Gen. Plant. **3:** 507. 1899.

III *Tremella nidus-avis* (Thaxt.) Arthur, Proc. Ind. Acad. Sci. **1900:** 136. 1901.

O, I *Aecidium nidus-avis* (Thaxt.) Farlow, Bibl. Index **1:** 68. 1905.

III *Gymnosporangium juvenescens* Kern, Bull. N.Y. Bot. Gard. **7:** 448. 1911.

The reasons for including *G. juvenescens* Kern as a synonym of *G. nidus-avis* will be presented in the sections to follow.

Crowell (1940) considered *G. effusum* Kern to be synonymous with *G. nidus-avis*, and thus has introduced a problem that must be dealt with. The writer has spent much time searching for *G. effusum* in South Carolina but has not been successful. However, the type material of *G. effusum* from the Arthur Herbarium has been very carefully examined and no close resemblance could be found between its telia and those of *G. nidus-avis*. In *G. effusum* the telia are elongate, broadly wedge-shaped, furcate, and according to Kern (1911) may become lacunose. In addition, the teliospores are very long, narrow, without an obvious constriction at the septum, and with no evidence of a slightly enlarged apex of the pedicel, characters which exclude this species from *G. nidus-avis*. To the writer, *G. effusum*, in its telial phase, is more closely related to the European *G. Sabinae* (Dicks.) Wint. than to any American species. Furthermore, preliminary cultures of *G. effusum* reported by Arthur (1912b) show that one alternate host is *Aronia*, and to check this many inoculations were made without success with *G. nidus-avis* on the known species and some varieties of *Aronia*. Therefore, because of the distinctive morphology of the two fungi and because of the differences in host ranges, it is not possible to include *G. effusum* as a synonym of *G. nidus-avis*. My own description of *Gymnosporangium nidus-avis* follows:

Spermogonia epiphyllous, hypophyllous or amphigenous, sometimes fructicolous, rarely caulicolous in yellowish, yellowish-orange or orange-yellow lesions, appearing on an average of twelve days after inoculation, the average size of the mature spermogonium being 111.7 × 86.7 μ.

Aecia following spermogonia on an average of twenty-one days after inoculation on the same host organs, the lesions 0.5 to 5.0 mm. in diameter

on leaves, usually with 1 to 6 cornute peridia which become up to 2.5 mm. in length. Peridia rupturing laterally or apically, finally becoming lacerate to or nearly to the base. Peridial cells typically lanceolate-oblong in face view remaining straight or nearly so when wet, 29.4–88.2 μ in length, 11.7–36.7 μ in width, thickness of side walls 2.9–5.8 μ, inner walls 5.8–11.7 μ, outer walls 1.4–4.4 μ; the outer walls of peridial cells are smooth, the inner walls with rugose-verrucose sculpturing, and the side walls rugose with interspersed verrucose markings. Aeciospores globoid to suboval, 14.7–36.7 $\times$ 11.0–27.9 μ in size; walls 0.7–5.8 μ thick, colorless to chestnut brown, smooth to minutely verrucose and usually with 8–12, rarely with 6 or 14 pores.

Uredia lacking. Telia foliicolous and caulicolous on dense or open fasciations of branches, or caulicolous on more or less enlarged branch or stem lesions; the ungelatinized telia pulvinate, hemispheric to oval, occasionally ligulate, of a color slightly darker than chestnut brown. Teliospores one to four-celled, usually with two cells, somewhat constricted at the septa, ellipsoid to oval in shape, 19.1–60.2 $\times$ 8.8–27.9 μ; walls smooth, hyaline to dark cinnamon brown, most often pale cinnamon brown, 0.2–2.2 μ thick with one to three pores usually with an obvious papilla; pedicels hygroscopic, often enlarging just below the apices, the enlarged portion occasionally rupturing, leaving the spore with a ragged fringe or collar.

GEOGRAPHICAL DISTRIBUTION

The geographical distribution of *Gymnosporangium nidus-avis* is limited only by the ranges of its telial hosts. This is true because the pomaceous hosts, according to Rehder (1940), are present throughout northern America and extend deeply into Mexico, while the *Juniperus* hosts are more restricted; therefore the aecial hosts need not be considered as factors affecting geographical distribution. The hosts of the telial phase of *G. nidus-avis*, as is clearly illustrated in the map below, show a nearly continuous and sometimes overlapping distribution in southern Canada and the United States, except in the southwestern limits of *Juniperus virginiana* and in the southeastern limits of *J. scopulorum*. Not shown on the map and only slightly extending the geographic range is the report of Hedgcock (1940) of *G. nidus-avis* on a new telial host, *J. barbadensis* from near Gainesville, Florida. This report has been confirmed by the writer who has examined a part of the specimen and has verified the determination of the fungus name.

On the map (Fig. 1) are shown the geographical ranges of *G. nidus-avis* and its telial hosts. The small circles represent the important stations where collections of the rust were made, and where specimens from these stations have been examined and verified by the writer, while the crosses represent stations reported in the literature that have not been verified but at the same time are believed to be accurate. Whenever possible,

material was obtained to verify reports given in the literature, especially when unusual characteristics for the specimens were cited.[4] It is believed, however, that intensive collecting will show that this rust is in every state and province within the range of the telial hosts. This assumption is based on the writer's observations which have extended over an area from Maine to South Carolina and westward to southeastern Tennessee and north central Ohio where it has been found to occur locally in most districts.

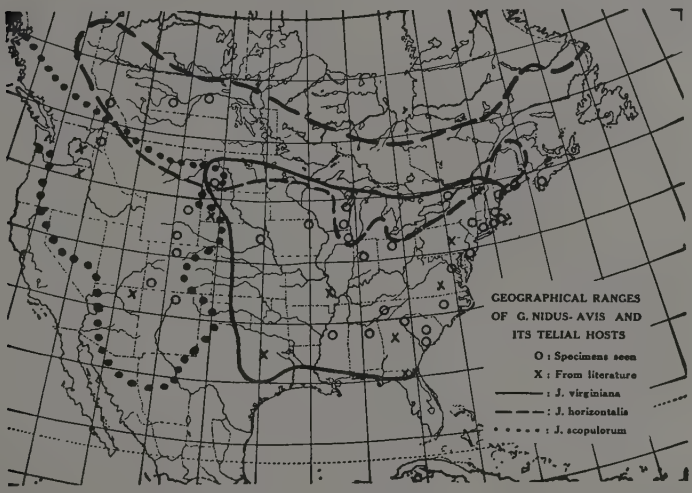


FIGURE 1. The Geographical Ranges of *G. nidus-avis* and its Telial Hosts. *Juniperus virginiana* L. including its var. *crebra* Fern. & Grisc. after Munns (1938); *J. horizontalis* Moench after Rehder (1940); *J. scopulorum* Sarg. after Sudworth (1915).

The local occurrence of this rust, in relation to its wide dispersal, is of interest and tends to confirm the reports of Kern *et al.* (1929) who stated that this fungus is rare in Pennsylvania, while Long (*in litt.*) and Coker (1920) respectively reported it as not uncommon around Washington, D. C., and Chapel Hill, North Carolina. Other reports in correspondence which have come to the writer bear out the above. Mrs. B. N. Brown was unable to find the rust in the vicinity of Marysville, Tennessee, although L. R. Hesler and the writer have observed this species in the vicinity of Knoxville, Tennessee. I. L. Conners was unable to find it around St. Catherines, Ontario; but in Saskatoon, Saskatchewan, the late Dr. W. P. Fraser indicated that it is rather common. R. W. Bailey was unable to locate the rust in the region around Ogden, Utah, while A. O. Garrett reported that it could be found several miles south of Salt Lake

[4] The report of Ray (1940) of *G. nidus-avis* from Oklahoma has been found to be based on a misdetermination and the specimen should be referred to *G. globosum* Farl.

City; J. L. Forsburg found it to be not uncommon near Fort Collins, Colorado, as did W. H. Long in the foothills of New Mexico; J. W. Hotson was unable to find the rust in the region around Seattle, Washington, while F. D. Heald indicated that this species was known only in its aecial phase around Pullman, Washington.

The reasons for the localized occurrence of this rust are not at all clear, especially when both aecial and telial hosts are in the same locality. However, from observations made during several seasons on Mt. Desert Island, Maine, it would seem that distance from the telial host limits the infection of *Amelanchier*. Evidence for this conclusion is furnished by the fact that although the different species of *Amelanchier* are common throughout the island, the only plants infected are within approximately 200 yards of *Juniperus horizontalis*, which is extremely local, being confined to the rocky ocean bluffs, and in addition is the only telial host. This is an excellent example of how the fungus may be limited to a small area, although in this instance the range is determined by the distance of the aecial host from the telial, and thus depends in part on the duration of viability in the basidiospores and in part on physiographic factors. This is in contrast to the findings of Thaxter (1891) and MacLachlan (1935b) who found that the basidiospores of other species could infect aecial hosts eight and six miles respectively from the source of inoculum. The writer's findings on Mt. Desert Island show that environmental factors may be more important in limiting the dispersal of this species.

An additional factor tending to limit local distribution is furnished by the relative period of maturation of the telial sori and the stage of development of the leaves of the aecial hosts.

Thus, in the vicinity of Clemson, South Carolina, species of *Amelanchier* are often found growing adjacent to cedars that are heavily infected with the rust. An abundance of telia was produced early in April, 1941, and gelatinization took place during four days of nearly continuous rain. At the beginning of this rainy period, several artificial inoculations were made on *Cydonia oblonga* growing in a sheltered habitat where the leaves had already begun to unfold, but at the same time the species of *Amelanchier* growing in the open had not yet started to produce leaves. On the plants artificially inoculated (*Cydonia*) the rust developed exactly the same as it did on this host at the University of Maine and in the Arnold Arboretum, yet on the species of *Amelanchier* not a single lesion was found that had resulted from natural infection. In 1942 and 1944 similar conditions reoccurred, and although artificial inoculations were successful on both *Cydonia oblonga* and *Amelanchier canadensis*, again no natural infections could be found. Here, then, is evidence that the aecial hosts must be in a condition favorable for infection, and this must coincide with the germination of the teliospores, all being more or less dependent on temperature and humidity, which confirms the conclusions of Crowell (1940).

While the examples cited above tend to explain that the viability of the spores, the physiography of an area, and the relative times of de-

velopment of foliage on the aecial hosts and telial sori may indeed play a part in the local limitation of this species, there are still other factors that have to be considered. Important among these are the effect of individual host susceptibility, and the occurrence of strains with varying degrees of virulence within this species of rust. Although there is no evidence from culture experiments that there are resistant strains of the *Juniperus* hosts, yet at any time field observations can be made which show that resistant hosts exist in quantities. As will be reported later, there is evidence resulting from culture studies that there exist resistant strains of the pomaceous or *Juniperus* hosts or both. In brief it can be stated that the species has a very wide distribution characterized by areas in which the rust is relatively scarce and in these areas the paucity of the species may be explained by one or more of the above sets of factors.

LIFE HISTORY STUDIES

SPERMOGONIAL PHASE

MACROSCOPICAL DEVELOPMENT

Heretofore very little has been published concerning the macroscopic symptoms and signs of infections caused by the spermogonial and aecial phases of *Gymnosporangium nidus-avis* on its pomaceous hosts. For recorded observations we are chiefly indebted to Thaxter (1887, 1889, 1891), Arthur (1901–1915), and Kern (1911), but for the main part these are brief and incidental to taxonomic delineations or limited life history studies of the fungus. They are also incomplete because of an insufficient number of specimens from the various hosts and geographic range of the fungus. Kern, in his monograph on *Gymnosporangium* (1911) was responsible for the enumeration of specific characters of *G. nidus-avis* and *G. juvenescens*, which at that time seemed sufficiently valid from the materials at his disposal, and which could not be checked from the life history studies then available. During the course of intensive studies of *G. nidus-avis*, the writer assembled a wide range of material from several geographical regions and carried out extensive series of culture experiments. Therefore it is possible at this time to give a more complete and connected account of the symptoms and signs of infections caused by this fungus on its pomaceous hosts than could have been done previously.

The first indication of infection, regardless of the organ affected, is a light spot or lesion in the host. These lesions soon change to a distinct yellow, then to a yellowish-orange which is more or less constant for most hosts. The lesions soon attain their definitive size and remain thereafter distinct from the adjacent uninfected host tissues, whether on leaf, stem or fruit. Subsequently, with the formation of spermogonia, the lesions lose their yellow color and become either orange-yellow or necrotic and black. Spermogonia appeared in from six to fourteen days in the writer's cultures. These organs occur singly or in a group of two to ten or more on

a single lesion. They are usually epiphyllous, occasionally hypophyllous or amphigenous on different lesions of the same leaf (Plate I, Fig. 3). In the early stages of development, the spermogonia are a waxy, orange-yellow on the lighter colored lesions. The waxy, colored appearance is caused by the colored spermatia in a viscous spermogonial fluid. The exudate is usually copious for the first five to ten days, during which time the general macroscopic symptoms normally remain unchanged, when flies and ants can be observed feeding on the exudate that has been shown by Rathay (1883) to contain sugars. As demonstrated by Craigie (1927), flies, attracted by the sweet spermogonial exudate, bring about cross-spermatization in *Puccinia Helianthi* and it seems probable that the insects mentioned above must perform the same function for this rust. It is probable also that the spermatia are transferred by water.

Following cross-spermatization, the exudate rapidly diminishes in amount and the ostiolar filaments turn a darker color. This change in color is the external indication that cross-spermatization has been completed, after which the exudate dries up entirely. During the period when spermatia are being produced, if the spermogonia are carefully examined, a definite protuberance can be seen emerging from the ostiole of each of these organs. These protuberances are made up of ostiolar filaments.

Along with the usual sequence of events in the ontogeny of the spermogonia, two distinct variations occur during the development of the infections. The degree of variation is dependent upon the host involved. Thus on *Amelanchier alnifolia* and *A. intermedia*, instead of the lesions being the usual yellowish-orange, they are reddish-orange with a yellowish-orange margin. The other important variation is the necrosis of lesions.

Necrosis as it is found in the lesions is variable and dependent upon the susceptibility of the host under attack. On the very resistant hosts, the lesions become necrotic soon after they develop. Indeed, this often takes place before the production of the spermogonia. However, occasionally some spermogonia are formed but these are small, and probably non-functional as is indicated by their failure to produce an exudate. Necrosis of the lesions occurred on the resistant and susceptible host species, like *Chaenomeles superba* and *Amelanchier stolonifera*, but on these it often may not take place until after the spermogonia and aecia are produced. When aecia are formed on these hosts some at least are non-functional, as is shown by the fact that the aeciospores produced did not germinate in tests. A very striking type of necrosis appeared on *Sorbus scopulina*, where the main part of the lesions remained alive, but a narrow zone at their periphery died.

MICROSCOPICAL DEVELOPMENT

Since the lesions and subsequent symptoms produced on the pomaceous hosts are the result of infection by the wind-carried basidiospores from the telia on the cedars, it seems desirable to follow more exactly the process

of infection and to study the subsequent development of the fungus within the host tissue.

According to MacLachlan (1935b) and other investigators, the basidiospores of *Gymnosporangium* species are carried by wind during humid spring weather. During this period the leaves of the alternate hosts are just beginning to unfold, and are often in their most susceptible condition. Therefore, when the basidiospores reach the host, germination proceeds, after a short delay, by means of germ tubes.

The germ tubes of the basidiospores may penetrate directly after germination of the basidiospores, or the germ tubes may grow to some length before they pass into the host, without the formation of appressoria, by penetrating the cuticle and becoming established intercellularly. From this it seems that the germ tubes must secrete a substance which dissolves the cuticle, thus permitting them to pass through this layer. Certainly the absence of appressoria seems to preclude the possibility of the fungus entering the host as a result of pressure exerted by the germ tubes. Infection takes place between twelve and forty-eight hours after inoculation, or perhaps even earlier under the most favorable conditions. The hyphae grow rapidly between the cells and the rust soon becomes thoroughly established in susceptible hosts. The intercellular hyphae vary considerably, but are usually 1.5–4.5 μ in diameter; they may often entirely fill the intercellular spaces and frequently appear to isolate an individual host cell from those adjacent. This fungus becomes intracellular only when haustoria are formed. In any stage of development after the fungus has become established, haustoria can be found in nearly all of the host cells in the lesion, large cells often having two or more haustoria which vary in shape from clavate, slightly curved to spiral.

Following the establishment of the fungus within a leaf, the spermogonial initials appear as knots of hyphae between the upper epidermis and the palisade layer or between the lower epidermis and spongy parenchyma cells. In this stage of development, two to six days after inoculation, the rust hyphae were seen to extend between the cells to a distance of a half-millimeter from the hyphal plexus. During subsequent development some of the hyphae in the center of the spermogonial initials elongate and appear to act as buffer cells which force the inner cell walls of the epidermis against the outer, and as a result of this pressure, the epidermis is forced outward. The buffer cells are soon replaced, however, by other fungal elements that arise from the young spermogonium. The writer's investigations indicate that the buffer cells play no part in the actual rupturing of the epidermis. This is accomplished by the continued growth of the spermogonium, while buffer cells seem to break down to make room for other developing spermogonial structures. The organ soon becomes differentiated into the spermogonial wall, from the bottom of which arise the spermatiophores and receptive hyphae, while at the same time the periphyses develop from the side wall. The spermatiophores are specialized, short hyphae, their function being to produce at their distal ends spermatia which are yellowish-orange,

ellipsoidal, and vary from 5.8–8.8 x 0.7–2.9 μ. The periphyses are hyaline, septate, subulate structures which vary in length from 58.8–133.8 μ. In addition to the periphyses are the receptive hyphae, but the latter structures arise from deep in the bases of the spermogonia instead of from the sides. The receptive hyphae are yellowish, uniform in diameter, non-septate, and have rounded apices (Plate I, Fig. 5) to which, as the writer has observed, spermatia fuse, but there was no evidence of the sub-cuticular receptive hyphae described by Allen (1930, 1932).

By the time the spermogonium ruptures the epidermis of the host, spermatia have already been produced in the spermogonial cavity. Spermatia may be liberated as early as six days after inoculation although the usual period is about twelve days, by which time the spermogonia are subepidermal and flask-shaped (Plate I, Fig. 3). After cross-spermatization has been completed, the spermogonial cavity becomes filled with elongated spermatiophores and dried up spermatial exudate, histological evidence that these organs have fulfilled their function.

The spermogonia have been used with success by Hunter (1936) as an aid in determining the various species or genera of the *Melampsoraceae*. With this in mind, it seemed desirable to make a comprehensive study of the spermogonia of *G. nidus-avis* and of *G. juvenescens* since the latter species has been accepted up to the present time. As is shown by measurements of one hundred medial sections, these organs vary in size from 80.8–171.9 μ high by 64.7–132.3 μ in diameter, the average size being 111.7 x 86.7 μ. The above one hundred measurements included fifty each of *G. nidus-avis* and *G. juvenescens*. The average dimensions of the *G. nidus-avis* spermogonia were 111.5 x 84.8 μ while those of the *G. juvenescens* were 111.5 x 88.9 μ. The evidence thus furnished by the nearly identical size and morphology of the periphyses, spermatia, and the size of the spermogonia, since these structures are relatively large, may accordingly be considered as showing only minute variations. Furthermore, the time of appearance of the spermogonia is the same in both species, and for this and the preceding reasons, *G. juvenescens* is considered to be the same as *G. nidus-avis*.

Earlier in this chapter I have described the external symptom of necrosis of some lesions. The histological symptomatology of the necrotic lesions was studied in detail. This was undertaken because it became necessary to determine whether or not necrotic lesions appearing on very resistant hosts were caused by *G. nidus-avis* or some other fungus. Even preliminary examinations showed that necrotic lesions caused by the rust fungus had what I have chosen to call an invasion zone (Plate I, Fig. 4). The invasion zone, showing the reaction of the host against the rust, is characterized by having a layer of host cells which are filled with a resin-like material that is yellowish in unstained sections, but in stained preparations takes dyes readily and stains deeply. The resin-like material appears the same in all respects as that to be found in the leaf spots where it is scattered throughout the infected area, whereas in the invasion zone of the necrotic lesions it is concentrated. Within the infected area of the leaf tissue the host cells may be

entirely dead while those of the healthy leaf tissues outside of the invasion zone are alive and have the usual arrangement of chloroplasts. Without exception, when the invasion zone was evident around necrotic lesions, rust hyphae could be found, but when the invasion zone was lacking, typical rust hyphae could not be found. Therefore, necrotic lesions on hosts that lacked invasion zones were considered to be caused by agents other than *G. nidus-avis*. Correlated with this is the fact that when there were necrotic lesions without there being an invasion zone on inoculated leaves, similar lesions also occurred on uninoculated leaves. Thus by using the presence of the invasion zone as a criterion for the presence of *G. nidus-avis*, it was possible to exclude necrotic spots caused by other fungi.

As others have previously suggested, plants are able in some degree to inhibit or prevent the growth of fungi. The presence of this invasion zone in the resistant plants would, then, appear to be a reaction by the host to prevent or limit the spread of the fungus since no hyphae were found beyond this barrier, whereas in susceptible host species in which no invasion zone is formed, the fungus hyphae can be seen well beyond the limits of the lesion.

AECIAL PHASE

MACROSCOPICAL DEVELOPMENT

The aecial phase starts at about the time the spermogonia are completing their function and becomes evident as a result of more or less hypertrophy accompanied by a change in the color of the affected host parts. The color of that part of the lesion from which aecia finally emerge is nearly always yellow, but frequently when the spermogonia are epiphyllous, the under side of the leaf does not turn yellow until the formation of the aecial fundament which is usually accompanied by hypertrophy. The amount of hypertrophy varies in degree and occurrence according to the relative susceptibility of the host, and according to the organ involved. In the more or less circular leaf lesions, no enlargement of the host tissue takes place until the aecia begin to form, at which time there is a slight swelling of the lesion from which a single aecium or several aecia finally emerge. The swelling is absent on resistant hosts where there is no indication of aecia even though spermogonia are present. Some hypertrophy is evident, however, if aecia do develop on resistant hosts; it is smaller when the aecia remain embedded, and larger when they emerge.

There are two general types of leaf lesions, their shape depending on their relative position with respect to the major veins. Most of the lesions occur in the thin parts of the lamina where there are no major veins and the size is influenced by the susceptibility of the host, it being smaller on the more resistant species and larger on the more susceptible. On *Amelanchier stolonifera*, a susceptible species, the spots vary from 0.5–2 mm. but on *Amelosorbus Jackii* (Plate I, Fig. 1), a very susceptible species, their diameters vary from 2–5 mm. When lesions occur on leaf veins, there is always some

hypertrophy, with the vein as its long axis. These swellings are usually hypophyllous, but may be evident on the upper leaf surface. A severe vein infection often causes a distortion of the leaf (Plate I, Fig. 2), and in addition the aecia may be amphigenous. Likewise, on affected fruits, the amount of hypertrophy is not readily assessed. Infected fruits are not much larger than the uninfected, but they are more or less distorted. When young stems become infected, there is also more or less distortion and a conspicuous enlargement (Plate I, Fig. 2). No comparison has been made in this discussion of the macroscopic symptoms of *G. nidus-avis* and *G. juvenescens*, because there were no variations in the developmental stages of the two species that could be distinguished.

MICROSCOPICAL DEVELOPMENT

The nuclear phenomena which occur during the transition from the spermogonial phase to that of the aecial phase have not been entirely worked out for any rust. Unfortunately the writer has not been able to contribute to the elucidation of this phenomenon, but it is postulated that cross-spermatization is followed by dicaryotization. This latter process may begin when the haploid nucleus of the spermatium has passed into the receptive hypha, and end when the haploid aecial fundament becomes dicaryotic. It is then that the aecial phase is initiated. This stage marks the beginning of a period of rapid development of the aecia which is correlated with a reaction of the host that is almost immediate. The apparent host reaction is to increase the size and number of the cells of the lesion. In this stage of development, hyphae are discernable considerably beyond the limits of the infection zone where there is no visible host reaction.

Aecial primordia, each consisting of a plexus of haploid hyphae, appear about the time the spermogonia are mature, are formed just below the palisade cells in the leaves. Aecial primordia appear about six days after cross-spermatization has been completed or about twenty-four days after inoculation.

The formation of the hyphal plexus is accompanied by a breaking down of host cells in the area, followed by the development of large thin-walled cells approximately at the center of the primordium. The aecial hymenium soon becomes visible in the lysigenous cavity formed by the dissolution of the thin-walled interwoven hyphae. The peripheral and apical cells appear as the initial peridial cells (Plate I, Fig. 6). The elongating peridium appears not to force its way out of the hypertrophied host tissue but to follow a path of rust hyphae which in turn seem to break down the host cells in advance of the apex. No evidence was found that would indicate that the host cells were forced to one side by the apex of the peridium or that the epidermis was actually split to allow the peridium an exit.

By the time the aecium reaches the surface of the host, the apical portion is filled with a mass of loose spores. Only those in the process of formation remain attached to the clavate sporophores. The peridium and the enclosed structures are all dicaryotic, whereas the hyphal plexus, which

surrounds the peridial envelope, is for the most part haploid. Since it is formed before dicaryotization, this hyphal plexus is considered to be of a more or less stromatic nature not properly belonging to the aecium. However, among the haploid cells there are some scattered hyphae which secondarily have become dicaryotic.

A careful study was made of the development and morphology of the peridial cells and aeciospores because these structures were supposed to show differences which enabled Kern (1911) and Arthur (1934) to distinguish between *G. nidus-avis* and *G. juvenescens*. The differences were to be found in the method of peridial dehiscence, in peridial cell morphology and aeciospore size.

My own observations show that the peridia, regardless of the origin of inoculum used for the cultures, may rupture apically soon after emergence, or retain their cornute form until after elongation has been completed. This phenomenon appears to depend upon whether or not they are alternately wetted and dried or whether dehiscence is retarded during a dry season. Cultures made with western material of *G. juvenescens* in Maine during 1938 developed exactly in the same manner as did the indigenous rust, *G. nidus-avis*. The peridia dehisced apically soon after their emergence and became lacerate to, or nearly to, the base. The same method of dehiscence occurred with the cultures that matured the latter part of June and early July 1939, in the Arnold Arboretum. However, cultures, regardless of the origin of the inoculum, that matured later during almost drought conditions, did not dehisce at all or only after collection. When the cornute form is retained by the peridia, rupturing first occurs laterally, followed by the rupture of the apex, after which the peridium becomes lacerate, its parts usually remaining straight or only slightly divergent. In some cases only the apex ruptures and the peridium retains its cylindric form. It was found that such peridia were made up of cells with finer markings than those peridia which become more lacerate. These findings do not agree with those of Kern (1911) and Arthur (1934) who reported that in *G. nidus-avis* the peridium ruptures apically and becomes lacerate to the base, while in *G. juvenescens* the peridium is tardily dehiscent at the apex, the rupturing first occurring laterally, and finally the peridium becomes lacerate nearly to the base. Because of the reported variation in the method of peridial dehiscence, an attempt was made to explain this by a careful study of the morphology of the cells of the peridium.

Kern (1911) described the peridial cells of *G. juvenescens* as "lanceolate-oblong in face view, 16–23 x 65–110 μ, linear-rhomboid in side view, 17–27 μ thick, outer wall rather thin, 1–1.5 μ, smooth, inner and side walls medium thick, 5–7 μ, finely and closely verrucose-rugose with irregular and oftentimes ridge-like papillae." Arthur (1934) added that the cells remain straight when wet. Kern (1911) described the peridial cells of *G. nidus-avis* as "lanceolate in face view, 15–23 x 55–88 μ, linear in side view, 14–18 μ thick, outer wall 1–1.5 μ thick, smooth, inner and side walls 5–7 μ thick, coarsely rugose with narrow ridges, with shorter often roundish papil-

lae interspersed." Arthur (1934) again added the important character that these cells remain straight when wet.

Fischer (1891 and 1895) and Kern (1910) pointed out that peridial cell markings were very important in differentiating between species of *Gymnosporangium*. I have made extensive observations on many different species of this genus and have likewise found this character to be the most dependable for taxonomic delineations.

The apparent differences between the peridial cells of *G. nidus-avis* and *G. juvenescens* as stated above are in the length, thickness, and wall markings. Accordingly, an attempt was made to confirm the constancy of these characters. Samples of peridial cells from cultured material were measured. The inoculum used to produce the aecial specimens originated from Saskatchewan, Colorado, Tennessee, Maine, Massachusetts, North and South Carolina. The dimensions measured were length, width, thickness and thickness of the side, the inner and the outer walls. Extreme variation was encountered in the lengths and widths of the peridial cells from all of the regions listed. Only cells from the side walls of the peridia with typical oblong-lanceolate shape were measured. The results of these measurements are recorded (Table 1) according to the *Juniperus* host from which the inoculum originated to produce the fungus.

TABLE 1. DATA ON PERIDIAL CELL DIMENSIONS OF *G. nidus-avis* TABULATED ACCORDING TO THE ORIGIN OF THE INOCULUM USED TO OBTAIN THE AECIA

Origin of Inoculum	Length μ	Width μ	Thickness μ	Wall Thickness Side μ	Inner μ	Outer μ
J. horizontalis Sask.	29.4–88.2	11.7–25.0	14.7–36.7	2.9–5.8	5.8–8.8	1.4–4.4
J. horizontalis Maine	29.4–88.2	11.7–25.0	11.7–36.7	2.9–5.8	5.8–11.7	1.4–4.4
J. scopulorum Col.	35.2–88.2	11.7–22.0	11.7–30.2	2.9–5.8	7.3–10.2	1.4–4.4
J. virginiana Mass.	36.7–88.2	14.7–23.5	11.7–33.8	2.9–5.8	7.3–11.7	1.4–4.4

No significant differences are evident that would separate the eastern from the western rusts. Fischer (1891) and Arthur (1934) used only the outer and inner wall measurements; therefore additional measurements were made using only those dimensions. This time cultures were obtained from inoculum from Maine and Saskatchewan on *Juniperus horizontalis*, Colorado on *J. scopulorum*, and Maine and Massachusetts on *J. virginiana* (Table 2).

TABLE 2. DATA ON OUTER AND INNER PERIDIAL CELL WALL MEASUREMENTS TABULATED ACCORDING TO THE ORIGIN OF THE INOCULUM USED TO OBTAIN THE AECIA

Origin of Inoculum	Wall Thickness Outer μ	Avg. μ	Inner μ	Avg. μ
J. horizontalis Maine	4.4–14.7	8.5	0.7–4.4	2.5
J. horizontalis Sask.	5.8–14.7	8.9	0.7–4.4	2.6
J. scopulorum Colo.	5.8–14.7	9.2	0.7–4.4	2.7
J. virginiana Maine	4.4–14.7	8.5	0.7–4.4	2.5
J. virginiana Mass.	4.4–14.7	8.4	0.7–4.4	2.7

Measurements of the thickness of the walls also confirm the data in Table 1, and hence these results offer further substantiation of the thesis that *G. nidus-avis* and *G. juvenescens* should not be distinguished.

Since the above biometrical studies show no reason for the separation of the two species, the investigations were carried further by careful comparisons of the sculpturing on the peridial cells. The usual markings observed on peridial cells regardless of the origin of the inoculum has been found to be rugose-verrucose. The side walls are rugose with some verrucose markings interspersed. The inner walls are rugose along the sides, these rugae being extensions from those on the side walls. The centers of the inner walls are usually covered with short ridge-like papillae and verrucose markings. The outer walls are smooth. The more resistant hosts tended to produce aecia with more verrucose-rugose peridial cells than were found on susceptible species. However, this was not constant enough to indicate an expression of the effect of the host reaction on the morphology of the fungus.

Just as the preceding peridial characters were studied, so have those furnished by the aeciospores. Since the aecia of both *G. nidus-avis* and *G. juvenescens* could be produced by inoculation on similar hosts, further attempts were made to distinguish the species by their spore characters. Therefore measurements were made of the spore dimensions and the thickness of the walls, while at the same time counts were made of the number of pores, and notations were made of spore wall color and markings.

No differences could be found in the color of the walls. The variation, regardless of the origin of inoculum ranged from hyaline through cinnamon to chestnut brown or even darker, although some peridia were found to contain nearly all hyaline spores. The number of pores were counted only when they could be seen distinctly and it was found that the usual number of pores per spore varied from eight to twelve, although very rarely spores with six or fourteen pores were found.

Similarly, other characters to be found in the aeciospores regardless of the origin of the inoculum show no significant differences which would warrant separating the two species. Thus the shapes of the spores range usually from globoid to suboval although in any sorus it is possible to find abnormal spores which are easily distinguished from those characterized as normal. Just as the normal shape of the spores varies within relatively narrow limits, so do the surface characters of the aeciospore walls. A large series of observations on this point leads the author to conclude that the spores may vary from smooth to minutely verrucose. Not only is there this variation in the spores from the same aecium, but even using the same spores, the appearance of the markings may vary with the mounting medium used, — in lactophenol the markings stand out when present whereas when the spores are mounted in water, the minutely verrucose spores may appear smooth. Although the presence or absence of markings on the walls of the aeciospores has served various authors for separating *G. nidus-avis* from *G. juvenescens*, the present observations demonstrate that such dif-

ferences are not significant. The thickness of the aeciospore walls is relatively constant regardless of the origin of inoculum used to produce the spores. On the basis of 408 measurements of both eastern material of *G. nidus-avis* and of spores cultured from Colorado and Saskatchewan inocula, it was found that the thickness of the walls of the former varied between 0.7 and 6.5 μ but with a mean of 2.99 μ, whereas walls of the aeciospores which were produced from western inoculum varied from 1.0–5.8 μ with a mean thickness of 2.7 μ, or a difference of only 0.29 μ between the averages. This difference is so small that it is not considered to be of any taxonomic value for the separation of the eastern rust from the western.

Since other characters of the aeciospores have proved of little value in separating the two species, a careful determination was made of the aeciospore dimensions. It was believed that these, if anything, might enable one to distinguish the two species in question by following the examples set by Levine (1923) who was able to distinguish physiological races of a rust, and Colley (1925) who separated two closely related species by the use of biometry. For these biometrical studies, notes and data were kept separate for all the kinds of inocula used throughout the cultural investigations. The data in Table 3 are based on aeciospores produced from eastern inoculum collected on *J. virginiana* var. *crebra* in Massachusetts, *J. virginiana* from North Carolina, South Carolina, and Tennessee, while the western inoculum was from *J. scopulorum* growing in Colorado and *J. horizontalis* growing in Maine and Saskatchewan. Since the inoculum from all sources was used on the same pomaceous hosts to obtain the aecia, it is believed that any differences between the eastern and western inocula would become evident. In Table 3 not only is there a comparison of the dimensions of aeciospores produced by the eastern and western inocula, but also differences within each of these series.

TABLE 3. AECIOSPORE SIZE IN RELATION TO THE GEOGRAPHICAL ORIGIN OF INOCULUM USED FOR AECIAL CULTURES

Origin of Inoculum	No. of Spores	Range of Lengths μ	Mean Lengths μ	Range of Widths μ	Mean Widths μ
East	500	17.0–32.0	23.4	14.0–26.0	20.3
West	500	17.0–33.0	22.9	11.0–26.0	19.6
Mass.	400	16.1–30.8	22.6	13.2–23.5	17.7
Maine	400	17.6–33.8	22.1	14.7–25.0	19.6
Sask.	400	14.7–35.2	23.5	11.7–27.9	19.3
Colo.	400	14.7–36.7	22.0	13.2–25.0	18.4
Average		14.7–36.7	22.7	11.0–27.9	19.1

In this comparison it can be seen that the ranges in the lengths and widths of the two sets of spore measurements are very similar, but what is more important is that the differences in mean spore lengths and widths are insignificantly small, the differences in the mean lengths being only 0.5 μ, while in the mean widths the variation between spores produced from the eastern and western inocula is only 0.7 μ. An analysis of the data in Table

3 shows that the greatest difference in the average spore lengths is between the spores produced from the Colorado and Saskatchewan inocula, the difference being only 1.5 μ. In the mean spore widths the greatest difference of 1.9 μ is between the aeciospores cultured from the Maine and Massachusetts inocula. In consideration of the large size of the spores, the variations seem of little consequence, especially since in a comparison of the aeciospores from the eastern inocula with those from the Maine and Massachusetts inocula, the difference between the mean lengths was equally as small, 0.5 μ, while in the spore widths the difference is 1.9 μ compared to 0.7 μ. Similar differences exist between the spores produced from the Saskatchewan and Colorado inocula. It is now possible to conclude that the aeciospore dimensions have no character which might permit the separation of *G. juvenescens* from *G. nidus-avis*. However, the minute tendencies toward variation do indicate the beginnings of biological specialization which becomes very evident when host susceptibility is taken into consideration, a subject which will be discussed in a following section. Here again is emphasized the very close similarity of the eastern and western rusts. Thus it is shown here as in the preceding paragraphs of this section that there are no differences either in the spermogonial or in the aecial phases which might be considered large enough to delimit *G. juvenescens* from *G. nidus-avis*. The careful comparison of the western and eastern rusts was carried to the telial phase which is to be considered in the section to follow.

THE TELIAL PHASE

MACROSCOPICAL DEVELOPMENT

Gymnosporangium nidus-avis has been confusing as a species not only in its aecial phase but also in its perfect or telial stage because of the variability in its manifestations on various species of *Juniperus*. The extreme in variation is shown in a statement by Arthur (1910) when he described a collection of stem inhabiting telia from South Carolina as having an appearance like a large *Tremella* and which was not accepted as a rust until it was examined microscopically. As the result of extensive investigations and observations, the writer has been able to coordinate the sometimes very diverse points of view and to extend the knowledge of the telial phase of *G. nidus-avis*. Observations have been made from Maine to South Carolina and west to Tennessee and Ohio and in addition numerous herbarium specimens from the entire range (Fig. 1) of the rust have been carefully examined.

The most characteristic symptom caused by the fungus *G. nidus-avis* is the production of a fasciation of branches which when seen from a distance resemble a bird's nest. These fasciations, being more commonly known as brooms, appear to have their origin when a terminal or lateral growing shoot becomes infected.

In this respect there are three expressions of fungus infection: the

first a very dense broom with the subulate or juvenile form of leaves (Plate II, Fig. 1), that may reach twenty-four inches or more in diameter, and become fifteen or more years old. Many of the branchlets, arising from about the same place on the main branch or stem, remain slender throughout the life of the broom and retain most of their acicular leaves. The second form of broom is similar to the first except that the foliage remains normal. They do not appear as compact because the leaves remain closely appressed to the branches (Plate II, Fig. 2). Just why some brooms have subulate and others scale-shaped leaves is not clear, but both forms of brooms have been seen on the same tree and rarely a broom with acicular leaves may be found with one branch retaining its normal foliage. The third symptom of infection is different in general aspect from the first two, it being characterized by the fewer, more widely separated branchlets which retain their scale-shaped or sometimes subulate leaves only at their extremities. The branchlets become somewhat enlarged in diameter and very rough. The first symptom of infection occurs commonly on *Juniperus horizontalis*, *J. scopulorum* (Plate II, Fig. 4), *J. virginiana* var. *crebra* [5] (Plate II, Fig. 1) and occasionally on *J. virginiana*; the second on all of these hosts, while the third type is the common one on *J. virginiana*, although sometimes it occurs on *J. virginiana* var. *crebra*.

The fungus does not confine itself to the brooms but often invades the supporting branch or stem and the mycelium may extend several feet away from a broom. In addition, branches (Plate II, Fig. 3) and old stems not associated with brooms may be infected. When branches and stems are attacked by *G. nidus-avis*, the effect on the morphology of the host may or may not be externally apparent. Small young branches and stems may be slightly enlarged in diameter, the bark is usually very rough with deep longitudinal and transverse fissures, or occasionally, as Dodge (1918b) has reported, the bark may actually be split open. Sometimes, however, young infected branches do not show enlargement, and the only external evidence of the fungus is the presence of telial masses or the oval scars left in the outer bark just after the telia fall. When infected stems and branches become older, there is considerable enlargement, and the deeply furrowed bark of the infected area may be seen. Hartley (1913) reported an exceptionally large trunk lesion six feet eight inches long, and another lesion where the fungus had continued to spread for thirty-two years after the bark in the center had died. Similar symptoms are not uncommon on old trees that have been infected for many years.

As there is a difference in the characters of brooms produced on the telial host, there is also a difference in the occurrence of telia on branches and stems. From observations and specimens examined, it has been found that on *Juniperus virginiana* the telia usually occur on leafless parts of branches and stems and this is apparently also true on *J. barbadensis*,

[5] The variety of *Juniperus virginiana* can be distinguished from the true species with characters described by Fernald and Griscom (1935).

since the only collection of *G. nidus-avis* on this host that has been made was on a branch. On *J. virginiana* var. *crebra* and *J. horizontalis* the telia occur on both leafy branchlets and the older leafless branches and stems, while on *J. scopulorum* no telia have been seen that were not associated with a broom. This latter was at first thought to be a coincidence, but a careful examination of all available specimens, both fresh and dried, failed to give any evidence that telia were formed away from the brooms, and, therefore, it was concluded that such telia do not occur, or if they do, only rarely. Long (*in litt.*) has confirmed this conclusion from his observations of this rust on *J. scopulorum*.

MICROSCOPICAL DEVELOPMENT

The external alterations in the host morphology are not usually a true indication of the extent to which the rust has spread through a given host. For this reason it is necessary to examine sections of the host microscopically to determine whether or not rust hyphae are present. Such investigations show that the mycelium is present throughout the host tissues of the dense brooms and the large, yellowish-orange hyphae can be found through the tissues of the bark where, in stems one to five years old, the intercellular spaces of the cortex are much larger than in uninfected stems, thus making this region somewhat thicker than normal. These intercellular spaces are often crowded with rust hyphae which are also in the phloem, and cambial region, and not uncommonly extend into the xylem along the medullary rays, by which they may reach the pith, and in addition hyphae can be seen occasionally in the tracheids. Hyphae often can be found also in the subulate leaves of brooms, but even when brooms have a normal foliage, the leaves are frequently invaded by the fungus. The mycelium may also extend several inches away from the broom into the supporting branch or in advance of a branch or stem lesion without causing external symptoms. During the invasion of the host, the fungus mycelium spreads more rapidly longitudinally along the main axis of the branch or stem than transversely. The rate of spread longitudinally, as shown by Dodge (1931) is at least six inches in three years.

The effect of the fungus on its telial hosts having been considered, a treatment of vegetative and reproductive stages of the rust, *G. nidus-avis*, in its telial hosts will be discussed in the paragraphs to follow.

The mycelium is yellowish-orange and very irregular in size but usually 3–5 μ in diameter, penetrating and branching between the host cells, sending the small clavate haustoria into the parenchyma cells of the host. The hyphae can be seen also in the intercellular spaces of the cortex on young stems and the spongy parenchyma of the leaves. At any time of year, but most commonly late in the fall, large knots of hyphae are produced which represent the earliest beginnings of the telial primordia. Their presence may be indicated externally by a slight discoloration, but usually they are invisible to the unaided eye. There seems to be a slight amount of growth in the hyphal knots which may well occur in brief warm periods during

the winter. In early spring, definite telial primordia can be seen under the phellogen of the stems and the epidermis of the leaves, and these rapidly mature during the moist warm weather so that the telia are fully developed at about the time the leaves of the alternate hosts are being formed, the exact time of year varying considerably within the geographic range of the fungus — by early March in Florida, but not until May or early June in Maine. It is especially interesting to note that in both Fort Collins, Colorado, and Saskatoon, Saskatchewan, these sori are completely developed in early May. The telia appear from the nodes, internodes and leaves on the dense brooms, regardless of host or whether the foliage is of the scale-like (Plate II, Fig. 2) or acicular form. On the open stag-horn brooms, however, they are mostly on the older leafless parts of the branchlets where the telia occur irregularly (Plate II, Fig. 3). This is also true as to occurrence and position of the sori on the leafless parts of branchlets in the dense brooms, and on branches and stems not connected with a fasciated portion of the host. On young branches with smooth bark, the telia emerge at the margins of telial scars of previous seasons or cause new lesions, while on older branches and stems, the telia emerge from between the fissures of the rough bark.

In reference to the characters of the telial sori, shape, size, and color are of significance taxonomically. The first two are the most constant, but while shape should be considered both before and after gelatinization, size and color are of importance only before this takes place. The telia, when in the fresh ungelatinized condition and when they occur on the leafy, fasciated or normal branchlets, are pulvinate, hemispheric or oval, or occasionally tend to be ligulate, but these sori always have smooth surfaces. Only rarely are the telia confluent on leafy shoots, but are commonly seen in this condition on leafless parts of branches and stems. The telia inhabiting these leafless bark surfaces are about the same in shape as those on the brooms but tend to be larger and often coalesce, giving rise to a narrow elliptical sorus. Ligulate telia are not uncommon on stems, but in this instance they are never furcate, rough surfaced, or lacunose, this combination of characters being descriptive of the telia belonging to *G. effusum* and not *G. nidus-avis*. The dimensions of the ungelatinized telia are 1–6.5 mm. in diameter and 0.5–5.5 mm. in height on brooms, while on leafless, scaly-barked branches and stems they are 3–5 mm. long, 3–6 mm. wide and 2–9 mm. high. Upon gelatinization, the telia enlarge considerably in height, but little in diameter and width or in length along the stem. The highest gelatinized telium measured was 16 mm. In this condition they are globoid, ellipsoid or sometimes ligulate. Dodge (1931) reported a telium at least two inches in length which is longer than any the writer has seen.

In addition to a study of the size and shape of the telial sori, their usual color was determined by comparison with standard color charts in Maerz and Paul (1930). Color is probably the most variable of the telial characters, but in the fresh condition just after emergence, it has been found to

be reasonably constant, regardless of the host or position on the host. It should be mentioned here that no telia appeared to be exactly chestnut or cinnamon brown in the ungelatinized condition as reported by Kern (1911) and Arthur (1934). By careful and repeated comparisons, the color of ungelatinized telia on *J. virginiana* were found to be "Coromandel," on *J. scopulorum*, "Cordova," and on *J. horizontalis*, "rustic brown." All three of these colors are slightly darker than chestnut. Fully gelatinized telia were determined to vary from a light yellowish-orange to a darker yellowish-orange or "Spa Tan." Telia repeatedly gelatinized become cinnamon-brownish. After one long period of gelatinization, such as during a continued rain or after three or four brief periods of extension, the telia drop from their host leaving oval scars which are at first yellowish-orange from the remaining mycelium. Sooner or later, however, the scars become covered by callous tissue formed by the host. Regardless of the host, while the telia are still attached or immediately after they fall off, the colored subtending tissue mentioned above is nearly always present. Telia that emerge from the fissures of old bark often drop off or dry up after gelatinization without leaving evidence of their presence.

Although the telia may be somewhat affected by changes in the substratum or by ecological conditions, the teliospores are little affected by these factors, and therefore offer many important taxonomic characters. Because of this, a study has been made of the spore development and morphology, and a separate investigation on the process of germination which includes basidium and basidiospore formation and the discharge of the latter (Prince, 1943). Fully formed teliospores can be found before the host tissue, which covers the telium, has been ruptured, but if specimens are collected early enough in the spring it can be seen that prior to the formation of the teliospores there are telial primordia, the ontogeny of which has been carefully described and illustrated by Dodge (1918a), who pointed out that the terminal cells of the primordia elongate three to five times their diameter and form buffer cells which are followed by teliospores that arise from penultimate cells. Upon the enlargement of the teliospores and elongation of the pedicels, the host tissue covering the telium is finally ruptured.

The mature teliospores are very irregular in shape, size, and number of cells. Their shape varies from ellipsoid, tapering at both ends, through oblong to oval with both ends more or less obtuse. The most common form of teliospore is ellipsoid with both the upper and lower cells tapering slightly, and almost without exception they are somewhat constricted at the septum or septa which when present divides the spore into two or more cells. The number of cells in each spore varies from one to four. Mesospores, characterized by being one-celled, are commonly seen among the spores of the telium while the three and four-celled teliospores are rarely seen. The smooth teliospore walls are usually pale cinnamon-brown but the walls of some spores may be hyaline while others are dark cinnamon-brown. Similarly, the thickness of the wall is variable also, ranging

from 0.4–2.2 μ. The walls of the two-celled teliospores have pores that are nearly always papilliate. The pores are located at the septa, except for the frequent presence of an additional apical pore in the upper cells. There are no basal pores in the lower cells. In spores with three or four cells, the pores are located as in the two-celled spores, while the pores are apical in mesospores.

At an early stage the pedicels become differentiated from the teliospores which eventually become septate and enlarge in diameter while the stipes for a long time retain their original diameter, but elongate. During the final stages of elongation, the wall of the pedicel becomes thickened and by the time the spore has matured it has become somewhat hygroscopic. The top of the pedicels just below the spores often enlarge in diameter but never become bulbous like those of *G. clavipes*. When the top of the pedicels do enlarge upon gelatinization, this may continue to the extent that the outer wall bursts leaving a ragged fringe attached to the base of the spore, but with the inner wall surrounding the lumen remaining intact and continuous with the lower portion of the pedicel which does not break away or deliquesce.

As is true with the characters of the aeciospores, those of the teliospores do not furnish evidence that would lead one to consider *G. juvenescens* to be distinct from *G. nidus-avis*, nor are there any valid differences that would separate the eastern from the western strains. The only character that might be considered valid is that on *J. scopulorum* the telia do not occur on the old branches and stems away from the brooms, whereas on *J. virginiana* the telia are produced on these parts of the hosts. This difference, however, cannot be accepted because on *J. horizontalis* the telia occur on both the leafy shoots of brooms and on branches not connected with brooms. In addition to these facts, the morphology and size of the telia are the same regardless of host, and therefore from investigations by the writer, *G. juvenescens* is not a valid species.

In a letter dated July 18, 1941, Dr. Long agrees with the author that *G. juvenescens* on *J. scopulorum* is the same as *G. nidus-avis*, but he writes that he has seen *G. juvenescens* causing brooms with normal needles as well as the acicular form "but in all cases the brooms were dense and not of the open type that is found in certain areas of the east." Dr. Long believes that the open type broom which occurs more commonly in the South on *Juniperus virginiana* may be caused by a different rust than that which causes the dense brooms that are more common on the northern cedars (*Juniperus virginiana* var. *crebra*). His basis for this belief is that he examined 3040 "eastern red cedar" trees in and near the District of Columbia. Of the trees examined, 382 were infected with *G. nidus-avis*. Data recorded according to the type of symptom produced showed that on the infected trees there were 58 trunk lesions, 1108 branch lesions, 484 brooms of the open type, and 1 "poor little broom" with acicular leaves on a stunted tree. During additional observations in Arkansas he found that the cedars there also had only the open type of brooms. Additional char-

acters, he believes, that distinguish the southern from the northern rust, are that his observations show that the bark under the telia is a golden yellow during the development and gelatinization periods of the telia and that there are many mesospores in southern telia. He seems to have compared his extensive observations of southern specimens with a single collection from Sharon, Massachusetts, and because the latter specimen lacked certain characters present in the others he believes they are different.

These differences are invalidated, first because he did not recognize the two kinds of eastern red cedars, *J. virginiana* and *J. virginiana* var. *crebra*, the former of which, as has already been pointed out in this work, usually forms open brooms when attacked by *G. nidus-avis*, while the latter usually has dense brooms under the same conditions. In addition, the true *J. virginiana* according to Fernald and Griscom (1935) may occur as far north as eastern Massachusetts, but is most abundant from the coastal plain of New Jersey south and westward. Thus the cedars in Washington, D. C., and Arkansas are well within the range of the true species and not the northern variety. Secondly, the orange coloration of the bark under the telia is characteristic for at least two species of *Gymnosporangium* in addition to *G. nidus-avis*. Thirdly, during the present investigations, the orange coloration under the telia has been observed on all the *Juniperus* hosts of *G. nidus-avis* studied by the writer in the field; and finally, mesospores are not uncommon in the telial sori regardless of host or locality. Therefore it seems evident that it is important not to separate *G. nidus-avis* into geographical species or varieties by the broom types, coloration of the host tissue under the telia, or by the presence of mesospores.

As a further test of the possibility that *G. juvenescens* could be distinguished from *G. nidus-avis* in the telial phase, it would be possible to do it on the basis of teliospore dimensions. Accordingly, the lengths and widths of one hundred spores were measured from each of seven geographical localities; the collections coming from the following species of *Juniperus* from the different localities:

J. horizontalis Moench.	Bar Harbor, Maine
J. horizontalis Moench.	Saskatoon, Saskatchewan
J. scopulorum Sarg.	Fort Collins, Colorado
J. virginiana L. var. *crebra* Fern. & Grisc.	Canton, Jamaica Plain, Norwood, and Waltham, Massachusetts
J. virginiana L.	Chapel Hill, North Carolina Clemson, South Carolina Montvale Springs, Tennessee

In addition, the measurements were based not on spores derived from a single telium, but from several telia on specimens collected or received while these investigations were in progress, and only spores from dried telia mounted in lactophenol were used. Thus it was possible to obtain

from each host and locality a good representation of the degree of variation in the size of the spore, the basis of the data in Table 4.

TABLE 4. THE SIZE OF TELIOSPORES OF *G. nidus-avis* FROM DIFFERENT TELIAL HOSTS AND LOCALITIES

Hosts	Spore Lengths in μ	Mean Lengths μ	Spore Widths in μ	Mean Widths μ
Juniperus				
horizontalis (Me.)	22.0–47.0	32.8	11.7–27.9	17.3
horizontalis (Sask.)	25.0–63.2	37.1	11.7–27.9	16.5
scopulorum (Colo.)	19.1–50.0	34.4	11.7–22.5	16.2
virginiana var. *crebra* (Mass.)	26.4–51.4	35.8	13.2–23.5	17.0
virginiana (N. C.)	23.5–55.8	38.3	10.2–25.0	17.4
virginiana (S. C.)	22.0–60.2	41.7	10.2–22.0	16.2
virginiana (Tenn.)	20.5–51.4	39.4	8.8–23.5	16.3
	Total Range in Spore Lengths	Mean Length	Total Range in Spore Widths	Mean Width
	19.1–60.2	37.07	8.8–27.9	16.70

An analysis of the data in this table shows that the greatest difference of 8.5 μ in the mean spore lengths occurs between spores from Maine on *J. horizontalis* and spores from South Carolina on *J. virginiana*. In the width measurements, the spores from South Carolina and those from Colorado on *J. scopulorum* have the same mean, and the greatest variation from these (1.2 μ) is in the spores from North Carolina on *J. virginiana*. There is certainly no evidence in Table 4 to show that *G. juvenescens* is different from *G. nidus-avis* when the mean lengths of the spores on *J. virginiana* var. *crebra* from Massachusetts differs only by 1.4 μ from those on *J. scopulorum* from Colorado, and the mean widths differ only 0.8 μ; the first comparison in the spores from the north and south seems to bear out Dr. Long's argument, yet even this is invalidated when an analysis of the data in Table 5 is made.

For the data in Table 5, the lengths and widths of fifty spores from telia on *J. virginiana* var. *crebra* were measured from each of twelve stations in Massachusetts. The telia are different from any used for the data in Table 4. All twelve stations are within a twenty-mile radius of Boston. First, it will be noted that there is nearly as great a spread in the mean lengths and widths of the spores produced on the one host within a limited area as was found throughout the whole geographic or host range of *G. nidus-avis*. Next, it can be seen that there is as large a difference (8.5 μ) in the lengths of the spores from Newton and Canton, which are only about ten miles apart, as there is between the spores from South Carolina and Massachusetts to which attention was called in the preceding table. Therefore it may be concluded that *G. juvenescens* cannot be distinguished

TABLE 5. THE SIZE OF TELIOSPORES FROM *Juniperus virginiana* VAR. *crebra* IN EASTERN MASSACHUSETTS

Station	Spore Lengths in μ	Mean Lengths μ	Spore Widths in μ	Mean Widths μ
Beverly	28.5–53.8	39.21	14.2–23.7	17.51
Medford	23.7–55.4	41.45	14.2–23.7	18.03
Brighton	23.7–45.9	36.86	11.1–31.6	20.41
Newton	22.1–42.7	34.96	15.8–25.3	20.25
Hammond's Pond Brookline	31.6–44.3	36.70	12.7–28.5	18.98
Chestnut Hill Brookline	25.3–49.0	39.39	11.1–23.7	18.82
Waltham	31.6–50.6	39.36	15.8–25.3	18.67
Jamaica Plain	26.9–44.3	36.38	15.8–23.7	18.04
Quincy	31.6–55.4	43.19	14.2–30.1	20.41
Walpole	25.3–50.6	37.02	14.2–26.9	20.41
Canton	31.6–53.8	43.51	14.2–28.5	19.78
Sharon	26.9–57.0	39.23	14.2–25.3	19.93
	Total Range in Spore Lengths	Mean Length	Total Range in Spore Widths	Mean Width
	22.1–57.0	38.76	11.1–31.6	19.30

from *G. nidus-avis* on teliospore size and neither can the southern rust be differentiated from the northern rust by this method. The total range in the teliospore lengths and widths of *G. nidus-avis*, then, may be said to vary from 19.1–60.2 μ x 8.8–31.6 μ, with a mean length of 37.9 μ and a mean width of 18.0 μ. In addition, after a comparison of average spore measurements in Tables 4 and 5, of the Massachusetts material, it can be seen that spore measurements from a single specimen or even one locality are not enough to give an accurate representation of spore size. For example, 35.8 x 17.0 μ (Table 4) is the average spore size for Massachusetts material because specimens from throughout the state have been included, whereas 38.8 x 19.3 μ, (Table 5) is representative of spores from only the eastern portion of the state. Moreover, neither of these are as accurate for the species as a whole as 37.1 x 16.7 μ in Table 4, this being the average size of spores from throughout the geographic range of the fungus.

THE HOSTS AND THEIR RELATIVE SUSCEPTIBILITY TO *G. NIDUS-AVIS*

Among the many problems facing the phytopathologists are the subjects of immunity and susceptibility of potential or actual phanerogamic hosts of the various rusts. The importance of these studies may be realized when it is noted that the alternation of hosts in the life cycles of some rusts gives the phytopathologist one of the few means of control of these fungi, since by removing one of the hosts to a safe distance, the alternate host

may be protected to a great extent. For this reason, then, the present studies were undertaken in order to determine what hosts are most susceptible to attack by the fungus and which are resistant or immune. From the information obtained during this study, it is now possible to state definitely which pomaceous trees may be grown near the *Juniperus* species and which are susceptible to *G. nidus-avis* and, therefore, unsuited for ornamental use. Thus the matter of planting horticultural projects may be undertaken with a degree of foresight not previously possible and with a consequent reduction of waste effort.

As far as can be determined from the literature, only a limited number of investigations have been carried out in order to determine the host plants of *G. nidus-avis*. The earliest records that we have are those of Farlow and Thaxter. Following these earliest records are those of Arthur, Kern and others who have increased the list of susceptible hosts. A summary of these investigations is given in Table 6.

In the above table the results of previous experiments on both *G. nidus-avis* and *G. juvenescens* have been tabulated in parallel columns to facilitate comparison. It can be seen that according to previous investigations it was thought that *G. nidus-avis* could be distinguished from *G. juvenescens* on only four hosts: *Crataegus Pringlei* and *Malus coronaria* as hosts of *G. nidus-avis* but not of *G. juvenescens*, and *Amelanchier intermedia* and *Sorbus americana* as hosts of *G. juvenescens* but not of *G. nidus-avis*. These and other purported differences have been considered sufficient to keep these two species distinct. However, it should be pointed out that when the results of different investigators are compared, there is an inconsistency which makes one question the advisability of such a distinction. It only needs to be pointed out that Prince and Steinmetz (1940) were able to inoculate successfully *Cydonia oblonga* with spores of *G. juvenescens* whereas Arthur (1912) was not. Similarly with *Malus pumila* var. *Wealthy*, Clinton and McCormick (1924) were able to obtain infection while Prince and Steinmetz were not, yet the writer in subsequent experiments was successful with his inoculations on this host.

In addition to the above brief discussion of previous investigations, it seems desirable to give a complete list of the pomaceous hosts of *G. nidus-avis* which includes those reported also for *G. juvenescens*.

Farlow and Thaxter, the two original investigators, were able to culture the rust successfully on only *Amelanchier canadensis* (L.) Medic., and an undetermined species of the same genus. Arthur, who reported cultures extending over the period from 1907 to 1915, successfully inoculated *Amelanchier erecta* Blanchard, *A. intermedia* Spach. *A. ovalis* Med., *Cydonia oblonga* Mill., *Crataegus Pringlei* Sarg., *Malus coronaria* (L.) Mill., *M. ioensis* (Wood) Brit., *M. pumila* Mill. var. *Whitney Crab*, and *Sorbus americana* Marsh. Kern (1911) reported additional hosts without cultures. They are *Amelanchier alnifolia* Nutt., *A. florida* Tindl., *A. oreophila* Nels., *A. polycarpa* Greene, and *A. pumila* Nutt. *G. nidus-avis* was reported by the same author as cultured on *Amelanchier vulgaris* Moench. Davis

TABLE 6

HOSTS	INVESTIGATORS	DATE	G.NIDUS-AVIS	G.JUVENESCENS	DATE	INVESTIGATORS
Amelanchier						
alnifolia				+	1924	Fraser
canadensis	Thaxter	1887	+	+	1907	Arthur
"	Thaxter	1889	+	+	1908	Arthur
"	Arthur	1910	-			
"	Dodge	1918	+			
"	Prince & Steinmetz	1940	+			
erecta	Arthur	1912	+	+	1909	Arthur
"	Arthur	1915	-	+	1912	Arthur
intermedia	Arthur	1908	+	+	1908	Arthur
laevis	Prince & Steinmetz	1940	+			
oblongifolia				+	1918	Davis
ovalis	Arthur	1912	+			
"	Arthur	1915	+			
stolonifera	Prince & Steinmetz	1940	+			
canadensis x A. stolonifera	Prince & Steinmetz	1940	+			
Wiegandii	Prince & Steinmetz	1940	+			
Aronia						
arbutifolia	Thaxter	1887	-			
melanocarpa				-	1907	Arthur
Chaenomeles						
japonica	Prince & Steinmetz	1940	-	-	1907	Arthur
Cydonia						
oblonga	Arthur	1912	+	-	1912	Arthur
"	Clinton & McCormick	1924	+			
"	Prince & Steinmetz	1940	+			
Crataegus						
coccinea	Thaxter	1889	-			
Pringlei	Arthur	1910	+	-	1907	Arthur
Malus						
coronaria	Arthur	1912	+	-	1912	Arthur
ioensis	Arthur	1910	+			
"	Clinton & McCormick	1924	+			
pumila	Thaxter	1887	-			
pumila var. Wealthy	Clinton & McCormick	1924	+			
pumila var. Wealthy	Prince & Steinmetz	1940	-			
pumila var. Whitney Crab	Arthur	1908	+			
Sorbus						
americana	Farlow	1886	-	+	1907	Arthur
"	Thaxter	1887	-	+	1909	Arthur
"	Thaxter	1889	-			
"	Prince & Steinmetz	1940	-			

(1918 unpublished) cultured the rust on *A. oblongifolia* Roem. Dodge (1918b) successfully inoculated undetermined species of *Amelanchier* and *Malus*. Clinton and McCormick (1924) cultured the rust on leaves of *Malus pumila* Mill. var. *Wealthy* in Petri dishes. Fraser (1925) successfully inoculated *Amelanchier alnifolia* Nutt. Arthur (1934) added to the host list without reference to cultures *Amelanchier Bakeri* Greene and *A. humilis* Wieg. Crowell (1940) reported *Malus fusca* (Raf.) Schneid.

while Prince and Steinmetz (1940) supplemented the host list of *G. nidus-avis* by means of cultures on *A. laevis* Wieg., *A. stolonifera* Wieg., and *A. Wiegandii* Nielsen.

In a consideration of the above data it is possible to state that *G. juvenescens* as a distinct species does not have a firm foundation, thus substantiating the conclusion arrived at as a result of the morphologic and biometric studies. However, the conflicting data already mentioned indicated the desirability of carrying on the investigations under conditions that were as near alike as possible. The facilities and extensive collection of living pomaceous hosts in the Arnold Arboretum of Harvard University offered an excellent opportunity to round out adequately our knowledge of the variation in susceptibility of the pomaceous plants.

As a source of inoculum, material was obtained from the following hosts and localities: — *Juniperus virginiana* var. *crebra* from Canton, Waltham, and Barnstable, Massachusetts; *J. virginiana* from Chapel Hill, North Carolina, Clemson, South Carolina, and Knoxville, Tennessee; *J. horizontalis* infected with the rust was obtained from Bar Harbor, Maine, and from Saskatoon, Saskatchewan. Brooms caused by the fungus on *Juniperus scopulorum* were obtained from Fort Collins, Colorado.

Immediately after collection or on arrival by post, the telial material was placed in a refrigerator which was maintained at a temperature of about 6° C. Under these conditions teliospores of New England material, freshly collected, would retain their viability up to six weeks. The teliospores of the southern material received by post, however, retained their maximum viability for only four weeks. After five weeks less than 50% of them would germinate. This fact made it necessary in the latter instance to use cuttings and potted plants forced in the greenhouse for inoculation experiments, because the spring season at the stations in the South from which the telia were sent was more than four weeks in advance of the spring season in Massachusetts. Cuttings were tried but they were not found to be satisfactory even though infection was obtainable on susceptible plants. For this reason potted plants of *Amelanchier stolonifera* and potted grafts of *Malus pumila* var. *Wealthy* were prepared in numbers for use during these investigations. These two hosts were chosen because in previous experiments the former was found to have been susceptible in all trials, the latter, because there was a question as to its actually being a host of *G. nidus-avis*.

The inoculum was prepared some time before it was to be used. Tests were made by observing the germination of spores in Van Tieghem cells or by observing the amount of germination of the teliospores just before the inoculum was used. Usually the latter method was followed because the percentage of viability of the teliospores when left *en masse* was more accurate than when the spores were separated and placed in Van Tieghem cells.

The inoculum was made by thoroughly wetting with distilled or rain water, the telial material to be used, and then placing the telia in a moist

container for at least two hours. Often material to be used for a forenoon's inoculations was prepared late the night before and left under cool conditions, that is, at 18 to 20° C. and by morning basidiospores would begin to appear. When cultures were to be made in the afternoon, telial material was placed in moist chambers early the same day, thus keeping a careful check on all inoculum used. When ready for use, a thick suspension of germinating teliospores was made in small, wide-mouthed, stoppered bottles from which inoculum was removed and painted on both sides of the leaves or on the surface of the fruits when the latter were present. All of the inoculated branches were protected during the infection period with celluloid cylinders similar to those described by Hubert (1916) but *Sphagnum* was used to plug the ends instead of cotton, and the chambers were then covered with paper bags after which the inoculated branches were marked with numbered tags. The paper bags served a twofold purpose. They protected the inoculated plant parts from the direct rays of the sun and prevented rapid evaporation from the *Sphagnum* plugs. Normally the chambers were allowed to remain in place from thirty-six to seventy-two hours, but during the unseasonably cold weather in the spring of 1940, they were left on for five days without causing injury to covered plant parts. After the chambers were removed, the suscepts were examined at frequent intervals until ready for collection, or until the subject was considered to be immune. In most cases, the plants listed as immune were observed for four weeks before a decision was made.

THE DETERMINATION OF VARIATION IN HOST SUSCEPTIBILITY

Considerable work has been done from the time of De Bary up to the present to determine the variation in susceptibility of economic plants to rust diseases, but nothing has been recorded as to the variation in susceptibility of pomaceous hosts of *Gymnosporangium nidus-avis*.

To express my observations with respect to this phenomenon, standards were established according to which data were recorded for these susceptibility studies. Five arbitrary categories were adopted; they are similar to those employed by other uredinologists but differ, through necessity, in some details. Their designations and descriptions follow: (1) *Immune*. No evidence of infection observed. (2) *Very resistant*. Necrotic spots produced, usually with some abortive spermogonia, always without aecia; the presence of an invasion zone clearly evident in a transverse section of the leaf (Plate I, Fig. 4). (3) *Resistant*. Lesions sometimes becoming necrotic; spermogonia and aecia taking longer to develop than on the more susceptible hosts. (4) *Susceptible*. Spermogonia forming within twelve days, aecia within four to five weeks; a few lesions occasionally becoming abortive or even necrotic; lesions with an average of one to five aecia. (5) *Very susceptible*. Time for the development of spermogonia and aecia about the same as in four; no lesions becoming necrotic; lesions with an average of six or more aecia.

As a result of the writer's investigation with artificial inoculations made in the Arnold Arboretum, it is now possible to add to the already rather extensive host list. These new hosts are *Amelanchier amabilis* Wieg., *A. asiatica* (Sieb. and Zucc.) Endl. var. *sinica* Schneid., *A. Bartramiana* (Tausch) Roem. x *A. laevis* Wieg., *A. florida* Lindl., *A. grandiflora* Rehder forma *rubescens* Rehder, *A. oblongifolia* Roem. var. *micropetala* Robins., *A. sanguinea* (Pursh) DC., *A. sera* Ashe, *A. spicata* (Lam.) K. Koch, *Amelosorbus Jackii* Rehder, *Chaenomeles lagenaria* (Thunb.) Lindl., *C. superba* (Frahm) Rehder, *Sorbaronia Dippelii* (Zab.) Schneid., *Sorbus americana* Marsh., *S. americana* var. *fructo-albo* auct., *S. americana* Marsh. var. *micrantha* Dum.-Cours., *S. Aria* (L.) Crantz var. *salicifolia* auct., *S. aucuparia* L., *S. aucuparia* L. var. *edulis* Dieck, *S. aucuparia* L. var. *xanthocarpa* Hartw. and Ruempl., *S. discolor* (Maxim.) Hedl., *S. japonica* (Decne.) Hedl. var. *callocarpa* Rehder, *S. latifolia* (Lam.) Pers., *S. scopulina* Green, and *S. thuringiaca* (Ilse) Fritsch.

It became obvious during the progress of this investigation that there were considerable variations in the degree of susceptibility of some of the hosts, not only in the different host species but also in different plants belonging to the same species. For this reason, all of the plants inoculated and found to be susceptible in some degree are listed in Appendix I and the variations in the susceptibilities of the hosts are indicated by symbols. The origin of the telia used for inoculum is shown with reference to host and geographical station.

Some plants, as *Amelanchier canadensis*, *A. humilis*, *A. sanguinea*, *A. sera*, *A. stolonifera*, *Chaenomeles lagenaria*, and *Sorbus scopulina* were found to exhibit the same degree of susceptibility to *G. nidus-avis* regardless of range of telial host. Other plants, however, show a variation in their reaction to the fungus. The cultures on *Amelanchier amabilis* tend to separate the eastern rust from the western. This host was found to be susceptible to the rust from Colorado and Saskatchewan, but was resistant to the rust from Maine, and immune to the rust from Massachusetts. The fact that there was a difference in the degree of susceptibility of the aecial host when it was inoculated with spores from widely separated localities, strongly suggests that different strains of the fungus have arisen through geographic segregation. Additional evidence of this is shown by inoculations on *Amelanchier grandiflora* forma *rubescens*, *A. oblongfolia*, *A. spicata*, *Amelosorbus Jackii*, *Sorbus americana* and other species listed in Appendix I.

The segregation of geographic strains is only one factor. A complication results from the fact that there is also evident a tendency for basidiospores from a given telial host to infect one pomaceous host to a different degree than do the basidiospores from another telial host. Here then is evidence of fungus strains. Thus, according to the results in Appendix I the rust strain on *Juniperus virginiana* can be distinguished on *Amelanchier asiatica* var. *sinica*, *A. Bartramiana* x *A. laevis*, and *Sorbus japonica* var. *callocarpa*. Similarly, the strain from *Juniperus horizontalis* can be separated on

Sorbus americana var. *micrantha* and *Amelosorbus Jackii*. Finally, the strain on *Juniperus scopulorum* can be separated on *Amelanchier florida*, *Amelosorbus Jackii*, and *Cydonia oblonga*.

While there is evidence that there is some host specialization, it does not seem that this should be taken to indicate the desirability of erecting large numbers of strains as has been done for the graminicolous species of rusts. In addition another examination of Table 6 shows clearly that experiments with a limited number of hosts may lead to false conclusions. Examples of this are shown by the inoculations on three plants of *Amelanchier spicata* numbers 5215–A, 12635–A, and 12635–C. In this instance *A. spicata* 5215–A is immune to the spores from *Juniperus horizontalis* from Maine, but is susceptible to infection by spores from the same host from Saskatchewan. Qn the other hand, *Amelanchier spicata* 12635–A and 12635–C are offspring from the same parent. This shows a variation in the susceptibility within an individual host species. The same phenomenon is shown in the hybrid *Chaenomeles superba* 13017 and 18184, and in the species *Sorbus aucuparia* 17264–A, 17682–D, 17682–C, and 17266–E. The concept is thus made more confusing by the fact that individual host species show variations in the degree of susceptibility.

In spite of the confusion that seems to be added by the factor of individual host variation in susceptibility, it is possible to coordinate these variables if we consider the average of all of the inoculated susceptible hosts to inocula from the four geographic regions. In addition, there is confirmation of the supposition that there are different strains of *G. nidus-avis*. Data showing the average degree of susceptibility of all the susceptible hosts that were inoculated are given in Table 7.

TABLE 7

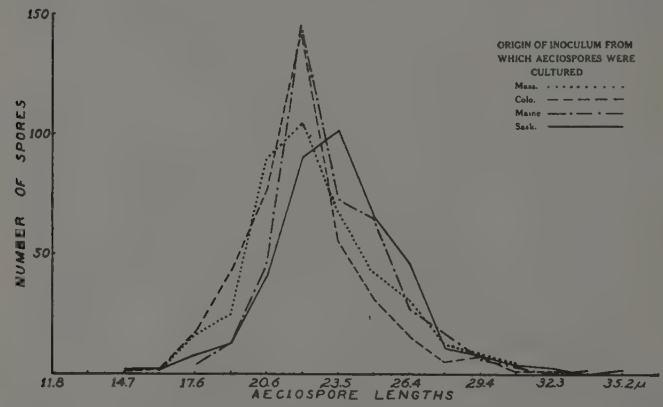
TABLE 7. DATA SHOWING THE AVERAGE DEGREE OF SUSCEPTIBILITY OF ALL OF THE INOCULATED SUSCEPTIBLE HOSTS TO FOUR DIFFERENT INOCULA

Telial Hosts	*J. virginiana*	*J. scopulorum*	*J. horizontalis*	*J. horizontalis*
Origin of Inoculum	Mass.	Colo.	Maine	Sask.
Degree of Susceptibility of Aecial Hosts	Percent	Percent	Percent	Percent
Very Susceptible	0	2	0	3
Susceptible	40	44	32	46
Resistant	19	10	26	21
Very Resistant	15	15	7	9
Immune	26	29	35	21

The above values mean that 2% of the inoculated plants were very susceptible to the rust from *Juniperus scopulorum*, 44% were susceptible, 10% were resistant, 15% were very resistant, and 29% were immune.

These data show that degrees of susceptibility or resistance are of the same order for all of the different inocula, but a slightly greater percentage of the hosts were immune to the inoculum from Maine than to the inocula from the other three stations. This confirms my interpretation of the data presented in the preceding table, that there is evidence of host and geographical strains of *G. nidus-avis*. There is also a slight variation in the degrees of susceptibility of the hosts to inocula from Massachusetts and Colorado, and Colorado and Saskatchewan. In addition, although the values given in Table 7 are expressed in the degrees of susceptibilities of the plants to the fungus, these values may also be interpreted as the ability of the fungus to attack these various hosts, since the same plants were used throughout.

The differences shown, even though slight, indicate that there is some



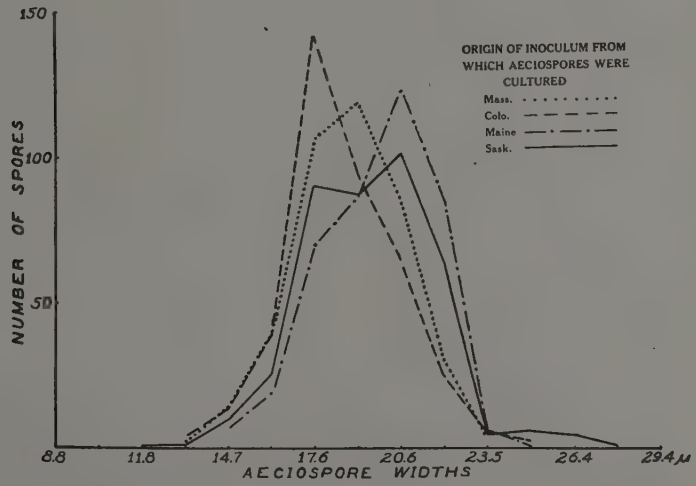
GRAPH A. A Comparison of Aeciospore Lengths. Aeciospores Cultured on Similar Hosts with Inoculum from Four Localities

variation in the virulence of these inocula when they are placed on the various hosts. There is still additional evidence of the presence of biological strains within *G. nidus-avis* to be found in the time necessary for development of the spermogonia and aecia. The data concerning this are presented in Table 8. Again the amount of variation in the host reaction to the fungus from different areas and different hosts is slight, but the variation, where it exists, indicates the presence of biological strains.

The sizes of the aeciospores furnish evidence of the presence of biological strains. The aeciospores measured came from cultures made with inocula from Maine, Massachusetts, Saskatchewan, and Colorado. The lengths and widths of these aeciospores are compared in Graphs A and B. The aeciospore measurements represented here are taken from the data given in Table 7. In Graph A where the spore lengths are compared, the

Massachusetts strain varies slightly from the Saskatchewan. Those from Maine and Colorado are very similar, but vary slightly from the two preceding strains. There is a greater degree of variability shown in the spore widths than in the lengths. Graph B illustrates this, and shows that the variability is not large enough to change the conclusions already drawn.

Even though the degree of variability shown by these comparisons is small, when one considers this variability and that which exists in the differences in aecial host susceptibility, and in the time of development, and finally, the variability in the manifestation of the symptoms of disease on the telial hosts, the only interpretation that can be advanced is that



GRAPH B. A Comparison of Aeciospore Widths. Aeciospores Cultured on Similar Hosts with Inoculum from Four Localities

there are definitely biological strains of *G. nidus-avis*. However, there is no evidence to show that more than one species is represented here, or that the one species can be separated into varieties or even forms. Certainly *G. juvenescens* has been shown to be morphologically identical with *G. nidus-avis*. More conclusive evidence which bears out this statement is that aeciospores from *Amelanchier grandiflora* forma *rubescens*, which were produced following an inoculation with basidiospores from telia on *Juniperus scopulorum*, were used to inoculate successfully *Juniperus virginiana* var. *crebra*, thus removing any doubt as to the ability of the fungus to infect both coniferous hosts, and thereby establishing the identity of *G. juvenescens* with *G. nidus-avis*.

In addition to the plants found to be susceptible to attack by the fungus, a number of the plants inoculated were found to be entirely immune. From

TABLE 8. A COMPARISON OF THE DEVELOPMENTAL PERIODS OF *G. nidus-avis* ACCORDING TO THE ORIGIN OF INOCULUM AND THE TELIAL HOSTS

Origin of Inoculum and Telial Host	Stage of Rust	First Appearance in Days	Average in Days
Maine	0	9–16	12.7
J. horizontalis	1	28–45	33.0
Saskatchewan	0	9–16	11.8
J. horizontalis	1	25–36	30.5
Colorado	0	10–16	13.3
J. scopulorum	1	25–41	33.7
Massachusetts	0	9–16	12.7
J. virginiana var. *crebra*	1	28–45	33.0
N. Carolina	0	6–14	8.9
J. virginiana	1	32	32
S. Carolina	0	14	14
J. virginiana	1	31–43	33.3
Tennessee	0	10–14	13
J. virginiana	1	31	31

the economic standpoint it is as necessary to know the immune plants as the susceptible. It is certain that any of the plants listed as immune could be planted adjacent to the susceptible species of *Juniperus* without danger of being infected by *G. nidus-avis*. However, persons interested in the planting of these combinations of hosts should keep in mind the works of Crowell (1934a and 1934b) and MacLachlan (1935a and b) who have dealt with other species of *Gymnosporangium* which infect both pomaceous and *Juniperus* hosts, since species found in the present studies to be immune to attack by *Gymnosporangium nidus-avis* may possibly be subject to infection by *G. Juniperi-virginianae*, *G. globosum*, or *G. clavipes*.

ECONOMIC IMPORTANCE AND POSSIBILITIES OF CONTROL

When compared with the three species of *Gymnosporangium* that commonly are called the cedar-apple rusts, *G. nidus-avis* is actually of little economic importance since only under most favorable conditions does it infect the apple trees. Yet even though it is of little importance in orchard practice, it is a fungus that must be taken into consideration by the landscape architect who employs both its aecial and telial hosts for ornamen-

tal plantings, often so close together that heavy cross-inoculations result that may cause severe damage to both hosts.

In the species of *Gymnosporangium* that cause the cedar-apples that are so conspicuous in the spring, it is the aecial hosts that are heavily damaged, whereas in the case of *G. nidus-avis* it is the telial host that suffers most. Dodge (1931, 1934) pointed out that cedars (*Juniperus* spp.) are actually killed following attacks by this rust, but Hartley (1913) indicated that when cedars succumbed following attacks by this rust, it was not the primary cause. Observations by the author support the views of Hartley rather than those of Dodge. It is clear, however, that the rust does cause considerable malformation of seriously infected trees, weakening them, and then by making openings in the protective corky bark, permits the entrance of wood destroying organisms. The most severely infected cedar tree that the author has had occasion to study occurs in the vicinity of Clemson, South Carolina. This tree is about eighty years old, as determined by increment borings, and has more than one hundred brooms. The trunk and branches are infected from the ground line upward so that in the spring when gelatinization of the sori takes place, the tree is nearly covered with the telia. In spite of this heavy infection, however, the tree shows no external symptoms of an early demise but when the increment borings were made, the first ten to fifteen years of annual growth at the center showed evidence of decay. Similarly, in several different localities where branches with brooms have been found dead or dying, the rust did not appear to be the primary cause, although there is the possibility that the fungus mycelium had penetrated beyond the obvious lesions and this in some instances may have resulted in partial girdling that so interfered with the vegetative activities of the broom as to weaken it during conditions that might have been adverse for the tree as a whole. Whatever may have been the cause of the death of the brooms, the result of infection by this fungus is to spoil the appearance by making distorted or malformed trees out of what would otherwise be symmetrical ornamentals.

The only course open to the tree surgeon or landscape gardener after a cedar has become infected, is to remove the broom as early as possible after it has become evident and possibly to remove infected parts near the point of attachment of the broom. Frequently this treatment may be inadvisable when a whole limb must be removed since the loss of a limb may damage the appearance of the tree more than the presence of an infected branch. Thus while tree surgery may in special cases prove to be desirable, the best method for preserving the health and beauty of ornamental cedar trees is to prevent their infection by not planting susceptible alternate hosts within three hundred feet, preferably more, of the host, and to practice control measures such as those suggested for *Gymnosporangium clavipes* by MacLachlan and Crowell (1937). The best method of all, where *Juniperus* and the pomaceous hosts must be planted near each other for desired effects, is to plant only pomaceous

hosts that have been shown to be immune, a list of which will be found in Appendix II. Among the names will be found a variety of shrubs and trees which should permit plantings with *Juniperus* species in almost any habitat and allow considerable latitude in the choice of types of trees.

SUMMARY

The first collection of *Gymnosporangium nidus-avis* was by Ravenel on *Juniperus virginiana* in South Carolina during 1848, while Farlow (1880) was the pioneer contributor to our knowledge concerning it, but not until 1891 did Thaxter establish this rust as a new American species. Arthur and Kern (1908 to 1915), Dodge (1918a–c) and Prince and Steinmetz (1940) were the main contributors to life history studies of this fungus; the latter two authors were unable to distinguish between the western *G. juvenescens* and the eastern *G. nidus-avis*.

A summary of investigations and the results obtained follows:

1. The taxonomy of the fungus has been clarified. As a result of morphological studies and inoculation experiments, it has been conclusively demonstrated that *G. juvenescens* is a synonym of *G. nidus-avis*.
2. The geographic distribution of its telial (*Juniperus*) hosts and aecial (pomaceous) hosts has been determined.
3. The symptomatology of the spermogonial, aecial and telial phases has been defined.
4. Results of studies on the microscopical development and morphology of the vegetative and reproductive phases in the spermogonial, aecial and telial phases are presented in detail.
5. The pomaceous host range and varietal host susceptibility has been clarified as a result of cultures with inoculum from four telial hosts representing seven localities, five eastern and two western.
6. The economic importance is considered, and possibilities of control of the fungus are presented.

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APPENDIX I. THE HOSTS OF *G. nidus-avis* AND THEIR VARIATION IN SUSCEPTIBILITY AS DETERMINED BY ARTIFICIAL INOCULATIONS

Hosts	Mass. *J. virginiana* v. *crebra*	Maine *J. horizontalis*	Colo. *J. scopulorum*	Sask. *J. horizontalis*	N. C. *J. virginiana*	S. C. *J. virginiana*
Amelanchier						
alnifolia 15700	S*		S			
amabilis 7058	I	R	S	S		
asiatica						
var. *sinica* 15694–C	R	S	S	S		
Bartramiana						
x *A. laevis* 4405	I	S	S	S		
canadensis 19100–B	S	S	S	S		
florida 11315–A	I	I	VR	I		
grandiflora						
forma *rubescens* 20678–A	S	S	S	VR		
humilis 6817	S	S	S	S		
intermedia 21920–B	S		S			
laevis 21447–B				VS		
laevis P–103–38	S	I	I	I		
oblongifolia 18265–A	S					
oblongifolia 18265–B	R	I	I	R		
oblongifolia						
var. *micropetala* 13192			R			
sanguinea 6620–B	S	S	S	S		
sera 11579	S	S	S	S		
spicata 5215–A	S	I	S	S		
spicata 12635–A	I	I	I	S		
spicata 12635–C	S		S			
stolonifera 644–30	S		S	S	R	
stolonifera (potted)	S	S	S	S	S	S
Amelosorbus						
Jackii 17943–B	R	S	VS	I		
Chaenomeles						
lagenaria 5098	S	S	S	S		
x *superba* 13017	I	I	I	I		
x *superba* 18184	I	I	VR	R		

* S = Susceptible; VS = Very Susceptible; R = Resistant; VR = Very Resistant; I = Immune

Numerals refer to Arnold Arboretum specimen numbers.

APPENDIX I (*continued*)

Hosts	Mass. *J. virginiana* v. *crebra*	Maine *J. horizontalis*	Colo. *J. scopulorum*	Sask. *J. horizontalis*	N. C. *J. virginiana*	S. C. *J. virginiana*
Cydonia						
oblonga 15648	I	VR	S	I		S
oblonga at U. of Me.		R		S		
Malus						
pumila						
var. *Wealthy* (potted)			VR		VR	
Sorbaronia						
Dippelii 170–25	I	I	I	R		
Sorbus						
americana at U. of Me.		I		S		
americana 22831	VR		VR			
americana						
var. *fructo-albo* 20931	VR					
americana						
var. *micrantha* 22381	I	R	I	R		
Aria						
var. *salicifolia* 222–27	VR					
aucuparia 17264–A	R	I	I	R		
aucuparia 17682–D		R		I	I	
aucuparia 17266–E	R	S	S	S		
aucuparia 17682–C	VR	VR	VR	VR		
aucuparia						
var. *edulis* 21427–A	VR	R	R	R		
aucuparia						
var. *xanthocarpa* 224–27	R		I	VR		
discolor 108–29–B	S	R	S	S		
discolor 20010	R	R	I	S	R	
discolor 21426–A				R		
japonica						
var. *callocarpa* 7703	S	I	I	I		
latifolia 19861–A	VR		VR			
scopulina 18452	R	R	R	R		
x *thuringiaca* 19847	R		I	I		
x *thuringiaca* 19847–B	I	R	R	R		
Number species and varieties inoculated	42	34	41	37	5	2

* S = Susceptible; VS = Very Susceptible; R = Resistant; VR = Very Resistant; I = Immune

Numerals refer to Arnold Arboretum specimen numbers.

APPENDIX II. A LIST OF PLANTS INOCULATED AND FOUND TO BE IMMUNE TO *Gymnosporangium nidus-avis*

Aronia
- *arbutifolia* (L.) Elliott
- *arbutifolia* (L.) Elliott forma *macrophylla* (Hook.) Rehder
- *melanocarpa* (Michx.) Elliott
- *prunifolia* (Marsh.) Rehder

Chaenomeles
- *japonica* (Thunb.) Lindl.

Cotoneaster
- *tomentosa* (Ait.) Lindl.

Crataegomespilus
- *grandiflora* (Sm.) Bean

Crataegus
- *austromontana* Beadle
- *Brittonii* Eggl.
- *chrysocarpa* Ashe
- *coccinioides* Ashe
- *crus-galli* L.
- *Douglasii* Lindl.
- *fecunda* Sarg.
- *Fischeri* Schneid.
- *Holmesiana* Ashe
- *intricata* Lange
- *macrosperma* Ashe
- *micracantha* Sarg.
- *mollis* Scheele
- *Oxyacantha* L.
- *phaenopyrum* (L.f.) Medic.
- *Pringlei* Sarg.
- *pruinosa* (Wendl.) K. Koch
- *punctata* Jacq.
- *rivularis* Nutt.
- *scabrida* Sarg.
- *spathulata* Michx.
- *viridis* L.

Malus
- *angustifolia* (Ait.) Michx.
- *arnoldiana* (Rehder) Sarg.
- *astracanica* Dum.-Cours.
- *baccata* (L.) Borkh.
- *baccata* (L.) Borkh. var. *Dartmouth Crab*
- *bracteata* Rehder
- *coronaria* (L.) Mill.
- *coronaria* (L.) Mill. var. *elongata* Rehder
- *fusca* (Raf.) Schneid.
- *glabrata* Rehder
- *ioensis* (Wood) Brit.
- *ioensis* (Wood) Brit. forma *plena* (Schneid.) Rehder
- *lancifolia* Rehder x "Mathews Crab"
- *platycarpa* Rehder
- *prunifolia* (Wild.) Berkh. var. *fructu-coccinea* auct.
- *pumila* Mill.
- *Sargenti* Rehder
- *Sieboldii* (Reg.) Rehder
- *Soulardii* (Bailey) Brit.
- *spectabilis* (Ait.) Borkh.
- *sylvestris* Mill.
- *Zumi* (Mats.) Rehder var. *calocarpa* (Rehder) Rehder

Mespilus
- *germanica* L.

Photinia
- *villosa* (Thunb.) DC. var. *sinica* Rehder & Wilson

Pyrus
- *amygdaliformis* Vill. var. *cuneifolia* (Guss.) Bean
- *communis* L.
- *nivalis* Jacq.
- *Pashia* D. Don
- *phaeocarpa* Rehder
- *serrulata* Rehder
- *syriaca* Boiss.
- *ussuriensis* Maxim. var. *hondoensis* (Kikuchi & Nakai) Rehder

Sorbopyrus
- *auricularis* (Knoop) Schneid. var. *bulbiformis* (Tatar) Schneid.

Sorbus
- *alnifolia* (Sieb. & Zucc.) K. Koch
- *americana* Marsh. var. *nana* auct.
- *Aria* (L.) Crantz
- *commixta* Hedl.
- *decora* (Sarg.) Schneid.
- *hybrida* L.
- *intermedia* (Ehrh.) Pers.
- *latifolia* (Lam.) Pers.
- *Matsumurana* (Mak.) Koehne
- *pohuashanensis* (Hance) Hedl.
- *rufo-ferruginea* (Schneid.) Schneid.

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EXPLANATION OF PLATE I

Fig. 1. Leaves and fruit of *Amelosorbus Jackii* infected by *G. nidus-avis*, the abundant, large lesions indicating the extreme susceptibility to inoculum from Colorado.

Fig. 2. Leaves and stems of *Amelanchier canadensis* bearing numerous aecia, evidence that this host is very susceptible to *G. nidus-avis* from Saskatchewan, Canada.

Fig. 3. Portion of a cross section of a leaf of *Amelanchier stolonifera*, illustrating amphigenous spermogonia of *G. nidus-avis*.

Fig. 4. Invasion zone bordering healthy tissue in portion of Wealthy apple leaf section. Note abortive spermogonium.

Fig. 5. A longitudinal section of a single spermogonium showing a darkly stained receptive hypha among the periphyses.

Fig. 6. A longitudinal section of a young aecium.

PLATE I

EXPLANATION OF PLATE II

Fig. 1. A dense broom caused by the telial stage of *G. nidus-avis* on *Juniperus virginiana* var. *crebra*.

Fig. 2. Foliicolous telia on leaves of *Juniperus horizontalis*.

Fig. 3. Caulicolous telia of *G. nidus-avis* on infected branch of *Juniperus virginiana*.

Fig. 4. A dense broom caused by the telial stage of *G. nidus-avis* on *Juniperus scopulorum*.

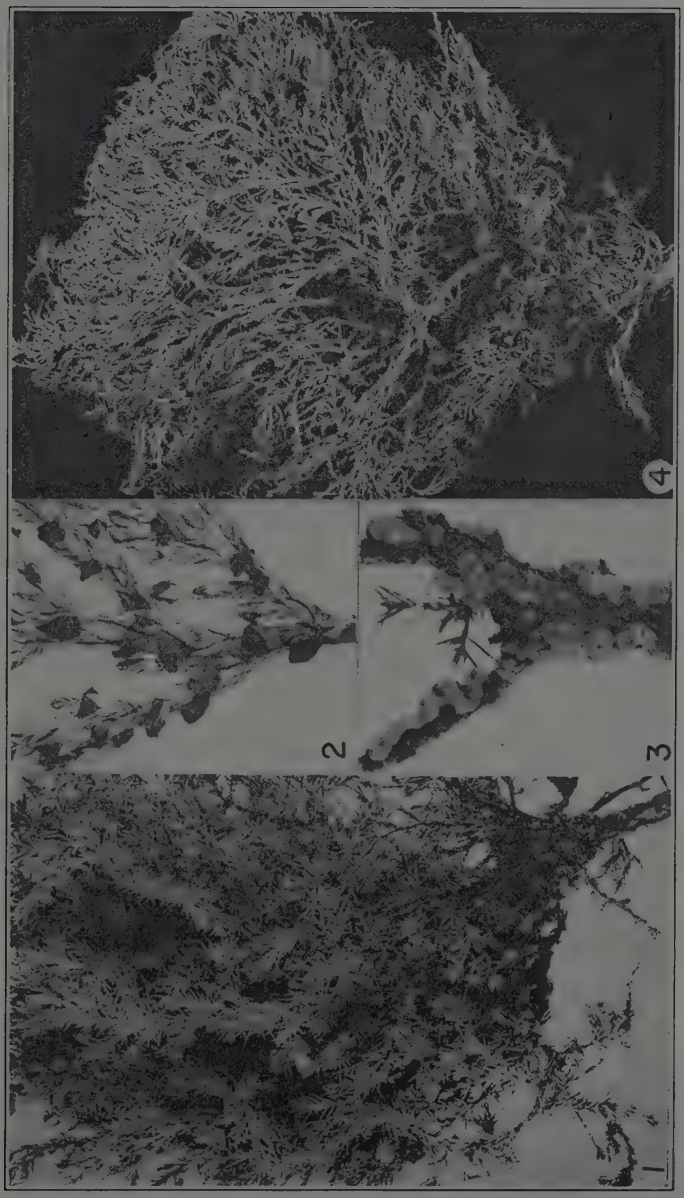

PLATE II

2(4):527–567 FARLOWIA JULY, 1946

THE BOLETINEAE OF FLORIDA WITH NOTES ON EXTRALIMITAL SPECIES

IV. THE LAMELLATE FAMILIES (GOMPHIDIACEAE PAXILLACEAE, and JUGASPORACEAE)

R. SINGER

As *Lenzites* is close to *Coriolus* in the Aphyllophorales, so, in the Boletineae, some lamellate families come closer to certain genera of the Boletaceae than other tubulose groups, *e.g. Paxillus* seems to be closer to *Gyrodon* than *Strobilomyces* or *Porphyrellus*. The relationship between *Paxillus* and the Boletaceae was actually recognized long ago, but the relationship between the Gomphidiaceae and the Boletineae had been doubted by some mycologists (including Gilbert), and it was necessary to draw attention to the similarities between these groups. (See Ann. Mycol. **40:** 555. 1942.) As for the Jugasporaceae, they seem to be intermediate, according to their characters, between the Boletineae and the Agaricineae (*Rhodophyllus*, Rhodogoniosporaceae; *Rhodocybe*, Tricholomataceae). For reasons we shall point out later (p. 548), we have always preferred to consider them as a family of the Boletineae.

The following monograph of the three families named above is written in the same pattern as the three preceding monographs on Florida Boletineae.[1] For a general introduction and a key to the families, the reader is again referred to Part I (Farlowia **2:** 97. 1945). In addition to the acknowledgments in my first monograph (*l.c.*), I wish to express my thanks to Dr. L. R. Hesler, University of Tennessee, and especially to Dr. A. H. Smith, University of Michigan, for the loan of important material of *Gomphidius* without which I would never have been able to prepare that genus for *North American Flora*, a manuscript on which the following treatment of the Gomphidiaceae of Florida is based.

GOMPHIDIACEAE R. Maire (1933)

Characters of the family: Pileus glabrous or tomentose or farinaceous, viscid to glutinose or more rarely dry, small to rather large; hymenophore lamellate, consisting of rather thick, decidedly decurrent gills with frequently obtuse edges (less so in subgenus *Chroogomphus*), waxy-subgelatinous to tender-fleshy consistency, and rather thick trama; lamellae subdistant to distant, more or less arcuate, gray to fuliginous when mature; spore print black; spores melleous to gray under the microscope, fusoid to subcylindric, smooth; cystidia large, projecting, usually distinctly incrusted, sometimes colored and with very thick walls (*Gomphidius to-*

[1] Singer, R. The Boletineae of Florida with notes on extralimital species. I. Farlowia **2**(1): 97–141. 1945; II. Farlowia **2**(2): 223–303. 1945; III. Amer. midl. nat. (in press).

mentosus), numerous to very rarely scattered (when old); trama of the gills more or less bilateral, not always clearly divergent, and very frequently partly interwoven, at least the hymenopodium interwoven but the trama never homogenously interwoven, nor intermixed, nor regular [2]); hyphae without clamp connections; stipe versiform, equal or swollen, etc., in most species and specimens with a discolored base which is pink or rich lemon yellow to orange yellow both inside and on the surface; veil present or absent, more often present, and then either entirely glutinous, or tender and fibrillose, or mealy and consisting of a loose pseudoparenchyma (*Cystogomphus*), sometimes forming an annulus; glandulae on the surface of the stipe present in one subgenus of *Gomphidius* (*Laricogomphus*); growing on earth and forming mycorrhiza with conifers, practically all species extratropical.

KEY TO THE GENERA AND THEIR SUBDIVISIONS

A. Veil consisting of spherocysts. Gen. *Cystogomphus*

A. Veil, if present, not consisting of spherocysts. Gen. *Gomphidius*

B. Context of the pileus ochraceous to orange (though at times in young specimens rather pallid), more rarely salmon to pink; veil constantly present, consisting of strictly parallel, pigment-incrusted hyphae, macroscopically never entirely glutinous, never hyaline; subhymenium filamentous-intermixed and dense to very dense; mediostratum rudimentary in young specimens, indiscernable in adult ones. Subgen. *Chroogomphus*

C. Pileus dry to subviscid in wet weather, not shining in dry weather, more or less tomentose to fibrillose. Sect. *Floccigomphus*

C. Pileus viscid in wet weather, shining in dry weather, not tomentose and not fibrillose except for traces of the veil on the margin. Sect. *Viscogomphus*

B. Context of the pileus white, more rarely pink to salmon, or becoming pink on exposure; veil absent, or consisting of subparallel-subinterwoven, thin hyphae which are not incrusted by pigment, macroscopically hyaline to white, and often entirely glutinous, sometimes blackening with age; subhymenium filamentous-cellular to filamentous, moderately dense; mediostratum of young specimens distinct, less distinct in older ones.

D. Veil visible only in the primordium, fugacious and not leaving any traces in adult specimens; dermatocystidia of the stipe fasciculate and the fascicles forming glandulae which make the stipe appear fibrillose or furfuraceous (though these macroscopical characters are not always easy to ascertain); mycelium (*of G. maculatus*) connected with *Larix*-mycorrhiza. Subgen. *Laricogomphus*

D. Veil covering the lamellae of the young specimens and leaving more or less distinct traces even in old specimens; dermatocystidia of the stipe not fasciculate, no fibrils or glandulae made up of dermatocystidia present on the surface of the stipe; mycelium in nature not connected with *Larix* but forming mycorrhiza with other conifers. Subgen. *Myxogomphus*

E. Spores (with the exception of immature and aborted ones) longer than 14 μ. Sect. *Macrosporus*

E. Spores, or majority of spores, shorter than 14 μ, or just reaching 14 μ. Sect. *Microsporus*

[2] See also observations for subgenus *Chroogomphus*, sect. *Viscogomphus*, p. 529.

Cystogomphus Sing., Ann. Mycol. **40:** 51. 1942.

Characters of the genus: these are evident in the key above. Type species *Cystogomphus Humblotii* Sing. No species is recorded in Florida.

Gomphidius Fr., Epicrisis, p. 319. 1938.

Characters of the genus: these are evident in the key above. Type species *Gomphidius glutinosus* (Schaeff. *ex*) Fr.

Subgen. **Chroogomphus** Sing., (in print).

Characters of the subgenus: these are evident in the key above. Type species *Gomphidius rutilus* (Schaeff. *ex* Fr.) Lundell & Nannf.

Sect. **Floccigomphus** Imai, Jour. Fac. Agr. Hokkaido Imp. Univ. **43:** 285. 1938.

Characters of the section: these are evident in the key above. Type species *Gomphidius tomentosus* Murr. Other species *G. sibiricus* Sing.; *G. leptocystis* Sing. In Florida none of these occurs.

Sect. **Viscogomphus** Imai, Jour. Fac. Agr. Hokkaido Imp. Univ. **43:** 284. 1938.

The characters of this section are obvious in the key above. The type species is the same as in subgenus *Chroogomphus.*

There have been various and seemingly controversial statements concerning the subhymenial and tramal structure of this section as compared with other sections. As for the trama, Fayod (1889) says it is bilateral quite generally in *Gomphidius*, and expresses surprise that De Seynes' figures do not show any bilateral trend. Lohwag (1937) finds the trama typically bilateral (truly bilateral as we call it in this paper) in *G. glutinosus*, and not distinctly bilateral, becoming irregular in *G. rutilus.* Elrod and Blanchard (1939) studied *G. maculatus* and found that the trama is "slightly and loosely interlaced, with a tendency toward a subparallel condition in many places. There is no sign of a differentiated mediostratum and laterostratum." In regard to the subhymenium the situation is still more obscure. Fayod (*l.c.*) says there is none. Lohwag (*l.c.*) and Singer (1942) state that there is one, and that it is pseudoparenchymatic in *G. rutilus*, and filamentous in *G. glutinosus.* Elrod and Blanchard (1939) and also Singer (1938) state that it is filamentous in *G. maculatus.* There is in all species, no doubt, a more or less definite layer immediately beneath the hymenium, but more recent re-examination by the writer tends to modify the above statements, and partly reverse them. It is true that in a not too thin section of the lamella of *G. vinicolor* the subhymenium appears to be coarsely cellular, but more detailed examination of the base of the hymenium shows a dense tissue of strongly interlaced, curved, irregular, strongly coherent hyphae which look cellular where they run for a short distance in a vertical direction. However, very few of the individual hyphae are short enough to be called subisodiametric and then they are very small, or very irregular, *e.g.* the widened hyphae from which two

branching hyphae arise, or the basal cells of the basidia. The subhymenium is not well differentiated from the underlying formation, and, in a sense, it may be stated that there is none. If we reserve the name subhymenium for a thin set of hyphae, continuing the basidia from their base downward, we cannot call it pseudoparenchymatic. *It is filamentous-intermixed.* As for the subhymenium of *G. glutinosus*, we may say that on superficial examination it always appears to be filamentous, but when the subhymenial cells are examined carefully and individually, they frequently turn out to consist partly of chains of very small globose bodies, and the same condition has been observed recently by the writer in *G. maculatus*.

The trama proper is not *a priori* different in *G. vinicolor*, *G. glutinosus*, *G. roseus*, and *G. maculatus* (the hymenophoral anatomy of *G. rutilus* does not differ from that of *G. vinicolor*). The difference pointed out by Lohwag and Peringer (1937) is not so striking, and more a matter of degree and of individual development. The mediostratum of *G. vinicolor* is very strongly reduced, so much so that no darker zone is seen in the pallid middle layer, called, as a whole, mediostratum by the above-cited authors. The irregular, interlaced accompanying zone between this and the subhymenium is called lateral stratum by all authors though I should think that it would rather deserve the name hymenopodium, since most of the looser central portion of the trama (Lohwag and Peringer's mediostratum) actually corresponds to the loose lateral stratum of the boletes. This will also make understandable the complicated tramal structure of *G. glutinosus*. In this latter species, we found a well-developed, melleous mediostratum, and there is no choice, in this case, but to call the hyaline looser layers at its sides the lateral stratum. The next-following layer between the lateral stratum and the subhymenium proper differs from the lateral stratum in being again more interlaced and dense. This layer is neither a part of the lateral stratum nor a part of the subhymenium. It is the hymenopodium. Lohwag and Peringer (*l.c.*) in the case of *G. glutinosus*, do not distinguish between this and the subhymenium proper, and, consequently, what they call subhymenium is the subhymenium plus the hymenopodium.

The gradual difference, therefore, between the trama of *G. glutinosus* and *G. vinicolor* (and *G. rutilus*) consists in the stronger or weaker development of the mediostratum proper on one hand, and the more or less decided tendency toward an irregular, interlaced condition in all or some layers on the other. It seems that other species may be intermediate between these extreme cases, for in my notes I described the trama of *G. roseus* exactly as it is in *G. glutinosus* though without mentioning the existence of a mediostratum, and as we saw above, Elrod and Blanchard did the same in the case of *G. maculatus*. However, it is obvious that the structure of the trama in the Gomphidiaceae, as in general in most Boletineae, is subject to drastic changes during the individual development of the carpophore, and our specimens may have been somewhat too old. Though the photographs published by Elrod and Blanchard do not show much as far

as the exact structure of the various layers goes, Lohwag and Peringer's figures 11–13 show this difference in different stages.

Another important fact not indicated in the literature on Gomphidiaceae, is the change in color of the spores when these are preserved in the herbarium for a considerable time. There is a specimen called *Gomphidius viscidus* [described here as *G. rutilus* (Schff.) Fr. ssp. *alabamensis*] collected ninety-five years ago and preserved in the Curtis Herbarium (FH) with a spore print on blue paper attached to it. The spores of the print are now ferruginous macroscopically, and greenish melleous under the microscope. This discoloration should be kept in mind when older herbarium material is described. I have never seen any of Fayod's specimens of *Gymnogomphus* Fay., but the description suggests that some old specimens of *G. rutilus* or of its group were misinterpreted and a new genus was created because of this fact.

KEY TO THE SPECIES

A. Mycelium pink-salmoneous; base of the stipe usually not markedly discolorous (yellow).

B. Middle portion of the cystidia strongly thick-walled, apex and base thin-walled. 1. *Gomphidius vinicolor* (in Florida: ssp. *jamaicensis*)

B. Middle portion of the cystidia not markedly thick-walled, wall of the cystidia nearly equal, thin to very slightly thickened (not more than 1.7 μ at most). *Gomphidius ochraceus*

A. Mycelium never pink-salmoneous, but pale yellowish white to "Isabella color"; base of the stipe frequently markedly discolorous, yellow. 2. *Gomphidius rutilus* (in Florida: ssp. *alabamensis*)

1. Gomphidius vinicolor Peck ssp. **jamaicensis** (Murr.) Sing. comb. nov.
Gomphidius jamaicensis Murr. Mycologia **10:** 69. 1918.
Gomphidius alachuanus Murr., Jour. Elisha Mitch. Sci. Soc. **55:** 367. 1939.

PLATE I, FIG. 4–7.

Pileus between "Natal brown" and "Army brown" with some tints of "light vinaceous cinnamon" to "Mikado brown" intermixed, or almost "chestnut," viscid, during dry periods "liver brown," "carob brown," or sometimes somewhat darker than these and shining, sometimes pallescent on the disk and becoming "Kaiser brown" or even "ferrugineous," glabrous, naked, smooth, conic-convex, then convex, eventually usually more or less flattened, or with depressed center, obtuse, (24)–50–(98) mm. diam. — *Hymenophore* between "Prout's brown" and "mummy brown," initially dirty ochraceous-alutaceous, eventually black from the spores, the lamellae broadest in the middle (4–10 mm.), subclose to subdistant, arcuate, decurrent, intermixed (one lamellula after either one or two through-lamellae), slightly transversely venose, only occasionally and very sparsely forked; spore print black. — *Stipe* "light vinaceous cinnamon" to "buff pink," or "vinaceous rufous," the base usually "cinnamon" to "clay color," "light ochraceous buff," or "ochraceous buff," sometimes at places becoming "Jasper red" or "orange cinnamon" to "cacao brown," not viscid, glabrous

except for the veil, smooth but more or less grooved when drying, naked, gradually tapering downward, or subequal, solid, 36–100 x 4–15 mm.; veil either forming a definite, fibrillose-woolly, narrow annulus which is concolorous with the remaining surface of the stipe, or reduced to a mere fibrillose zone at the apex of the stipe; mycelium pink. — *Context* of the pileus and upper portion of the stipe "pale ochraceous salmon" to "ochraceous salmon," or "pinkish buff" in pileus and "cinnamon buff" in upper part of stipe, in the base "primuline yellow" with a tinge of "yellow ocher" or "clay color," often somewhat umber immediately below the cuticle, fleshy, rather firm, not as soft and watery as in *G. glutinosus*; odor none, or agreeable when quite young, recalling apples or apple sauce; taste mild.

Spores melleous-grayish to gray, varying from a pure cinereous to fuliginous gray, ellipsoid to fusoid, not cylindric, smooth, (in carpophores with the spores of small average size, the short spores are usually the broadest, and the long ones the slenderest), 17–21.8 x 5.8–8μ; *basidia* (2)–4–spored, 34–46 x (8.2)–9.2–13μ; *cystidia* numerous, on edge as well as on sides of lamellae, slightly incrusted on the inside of the walls in many of them, the incrustation melleous, and in almost all of them there is a strong resinous or occasionally granular, fulvous-castaneous incrustation that covers the apices, otherwise smooth, thick-walled, the wall hyaline, thinner or quite thin at the apex which is frequently capitate, rarely clavate, and always broadly rounded, cylindric or slightly fusoid below, and there the walls reaching 2–5.5 μ in diameter but becoming thin near the very base, the entire length varying between 115 and 150 μ, the diameter from 13.5 to 22.5μ, the base reaching into the lateral stratum, the upper portion projecting well beyond the level of the sterigmata; *subhymenium* filamentous-intermixed; *trama* consisting of an indistinct mediostratum reduced to a central string of a few parallel or subinterwoven hyphae which are all hyaline and cylindric, but most of the trama proper (i.e. excluding the hymenopodium) formed by a hyaline, loosely arranged, partly subirregular layer that with age becomes homogeneous and increasingly irregular while any trace of a mediostratum disappears; *hymenopodium* obscured and thickly covered by an adhesive (sordid melleous brown) pigment that precipitates in form of an amorphous intercellular pigment when the preparation is boiled in 10% KOH, differing in this regard from the trama proper, and differing, also, in its much denser arrangement, the hyphae being more variable in diameter and running in all directions to form a subintermixed broad zone along the subhymenial layers; all *hyphae* without clamp connections; *pellicle* of repent, subparallel-interwoven, with fulvous-castaneous incrustation, elongate, clampless hyphae; *mycelium* consisting of filamentous hyphae which are beset with button-like ornamentations.

Chemical reactions: **KOH** on pileus, little reaction; on context, between "pale rosolane purple" and "thuilite pink," becoming "spinel red"; in base, "rich brown." — **NH_3**–vapors on context, "liseran purple" and "pale rosolane purple"; in base olive. — **NH_4OH** on pileus, little reaction; on

context between "pale rosolane purple" and "thuilite pink," becoming "spinel red"; in base brownish. — **H_2SO_4**, little reaction but the treated portions of the base becoming deep fulvous yellow when dried subsequently. —**$FeSO_4$** in all parts, "deep olive" to "dark olive."

Habitat: In woods, in Florida under *Pinus taeda*, possibly also *P. australis*, and *P. palustris*, but not observed in pure stands of any of the latter species; on sandy soil, gregarious, fruiting from November to January.

Distribution: North Florida and Alabama, also in the West Indies (Jamaica).

Material studied: **Fla.:** Alachua Co., Gainesville, *Murrill et al. F 10213*, *F 18431*, *F 20040* (all FLAS, *det.* Murrill); Planera Hammock near Gainesville, *Murrill et al. det. Murrill F 19517*, *F 20086* (FLAS) **type** of *G. alachuanus*, Newnan's Lake, East of Gainesville, *West & Murrill F 18402* (FLAS); my own collections compared with the type and partly from the type locality: *F 1657*, *F 1657a*, *F 1657b*, *F 1657c*, *F 1657d*, *F 1657e* (all FH). — **Ala.:** Lee Co. Auburn, Fall 1897, *F. S. Earle & C. F. Baker* (*G. viscidus*) (NY). — **Jamaica, W.I.:** Cinchona, in 5000 ft. elevation, *Earle* (*352*), **type** (NY).

This species is divided into several geographic races and mycoecotypes (in the sense of Singer, Sovietsk. Botan. **1940**, (5–6):262–269). The subtropical (*G. alachuanus*) and tropical-montane (*G. jamaicensis*) form, having subclose to subdistant lamellae and forming mycorrhiza with pines of the section *Australes*, should properly be called ssp. *jamaicensis* while the northern and western forms occurring with such pines as *Pinus resinosa*, and *P. radiata*, and differing morphologically in having more distant lamellae and frequently umbonate pileus, should be distinguished under separate subspecific names. The northern subspecies of *G. vinicolor* Murr. has the same characteristic cystidia with thick walls in the middle portion as has been observed in the southern form. It should not be confused with *G. ochraceus* Kauffm. and allied forms such as *G. superiorensis* Kauffm. & Sm., which also have pink mycelium and similar colors under certain conditions and in certain stages, but lack the thick cystidial walls. *G. tomentosus* Murr., which has thick-walled cystidia, has the walls nearly equally thick over the entire length of the cystidia, and not merely in the middle. *G. rutilus* and allied forms (ssp. *alabamensis*, the form called *G. furcatus* by Kauffman *non* Peck) is easily distinguished by the color of the mycelial tomentum and the thin-walled cystidia.

2. **Gomphidius rutilus** (Schaeff. *ex* Fr.) Lund. & Nannf., Fung. Exs. Suec. 409. 1937.
Agaricus rutilus Schaeff. ex Fr., Syst. Mycol. **1:** 315. 1821.
Cortinaria rutila S. F. Gray, Nat. Arr. Brit. Pl. **2:** 629. 1821.
Gomphidius viscidus (L. *ex*) Fr., Epicrisis, p. 319. 1838.
Paxillus pubescens Ellis, Bull. Torr. Bot. Cl. **6:** 76. 1876. (= ssp. *alabamensis*)
Gomphidius testaceus (Fr.) Britz., Hymen. Südbay. **4:** 133. 1885. (=var. *testaceus*)
Gomphidius litigiosus Britz., Hymen. Südbay. **9:** 14. 1893. (= var. *litigiosus*)
Gomphidius alabamensis Earle, Torreya **2:** 54. 1902. *nomen nudum* (= ssp. *alabamensis*)
Gomphidius viscidus forma *columbiana* Kauffm., Mycologia **17:** 122. 1925.

Ssp. **typicus.**

The type subspecies, the most common *Gomphidius* in Europe and in parts of the Rocky Mountain region, does not occur in Florida. It differs only slightly from the following subspecies (*alabamensis*) in having the pileus almost constantly umbonate, and in its geographic area.

Var. **testaceus** Fr., Epicr., p. 319. 1838 (*ut varietas G. viscidi*)

This is a small umbonate form with very light, almost white mycelium, and with the stipe lacking the yellow color of the surface and of the context. I have collected it under pines in mixed beech woods in Europe, but not in this country. Good typical specimens are preserved in the Hoehnel Herbarium (FH), from Tullnerbach-Pressbaum, Wiener Wald, Austria (*F. v. Höhnel B 1467*). The specimens described and illustrated under the name of *Gomphidius viscidus* var. *testaceus* Fr. in *Icones Farlowianae*, pl. 70, are a form of *G. ochraceus* Kauffm. *G. viscidus* fa. *testacea* Kavina seems to belong either to var. *pulcher* or var. *fulmineus*.

Var. **pulcher** Killerm. Denkschr. Bay. Bot. Ges. **21:** 58. 1940 (*ut varietas G. viscidi*)
Var. **litigiosus** (Britz.) Sing. comb. nov.

These two varieties, with differently colored pilei, are both described from Bavaria, not reported from America.

Var. **fulmineus** Heim, Treb. Mus. Ciènc. Nat. **15:** 68. pl. 1, *fig. 3.* 1934 (*ut varietas G. viscidi*)

This was described from Spain; it is possibly specifically different.

Kauffman described a f. *columbiana* which, as he thought, represents the American form of *G. viscidus* (*G. rutilus* ssp. *typicus* in our nomenclature). However, the examination of his herbarium shows that he mixed two different species under this name, one being an umbonate form of *G. ochraceus*, the other (including the type specimen) being *G. rutilus* ssp. *typicus*. It appears that Kauffman was under the impression that the European *G. rutilus* always is a large plant, which is definitely not true. Thus there remain only two differences between the European and the American form which escaped Kauffman. One is the frequently brighter color of the base of the American specimens, a character that aside from its vagueness does not seem to be quite constant. The other is a phytosociological character which could possibly be physiological: the American form is associated with pines of the series *Insignes* while the European form is associated with pines of the series *Lariciones*. If it could be demonstrated by experiments that the European form does not form mycorrhiza with *Pinus contorta* as readily as it does with *P. silvestris*, it would make the American form a mycoecotype lacking morphological differences (comparable with the races of rusts). However, as long as such physiological differences have not been shown, I prefer to list f. *columbiana* as a plain synonym of *G. rutilus* ssp. *typicus*.

Subsp. **alabamensis** (Earle *ex*) Sing. subsp. nov.

Gomphidius alabamensis Earle, Torreya **2:** 54. 1902 (*nomen subnudum*)
Paxillus pubescens Ellis, Bull. Torr. Bot. Cl. **6:** 76. 1876.

PLATE I, FIG. 1–3.

Tomento myceliali cremeo-albo vel melleo-isabellino; basi plerumque laete flavo in siccis; umbone plerumque nulla; cystidiis tenuitunicatis, incrustatis; ceterum *Gomphidio rutilo* et *G. vinicolori* analogus.

Pileus "light russet vinaceous," "cinnamon buff," "vinaceous cinnamon," "testaceous," sometimes reaching "chocolate," "Hay's brown" or "dark vinaceous brown," assuming at times colors like "pecan brown" or "purplish vinaceous" after drying, usually a lighter reddish-brown in dried specimens than *G. jamaicensis*, glabrous, more rarely with cracking pellicle showing orange flesh between the fragments, viscid, naked, shining when dry, convex to plane, eventually often depressed and turbinate, obtuse, rarely indistinctly umbonate, 30–100 mm. broad, mostly between 30 and 70 mm. — *Lamellae* "avellaneous," "clay color," "ochraceous tawny," later "testaceous," "snuff brown," or "sayal brown," and finally darker sooty from the spores, arcuate, then descendant, broad, subclose to distant, entire, thick, inserted with very short ones, occasionally some forked near the stipe, decurrent. Spore print "hair brown" to "deep grayish olive" in thin to moderate layer, very nearly black in good print. — *Stipe* varying from sordid whitish to "Congo pink" or subconcolorous with the veil which is "ochraceous buff" or "capucine buff," or streaked with vinaceous brown to almost tawny, with a bright yellow color very often at the very base of the dried stipes, mycelium cream-white to melleous-yellow or "Isabella color," strigose, the upper surface fibrillose and often showing a cortina-like annulus at the apex, glabrescent below, the veil often spurious, the outer fibrils somewhat slippery-sticky-subviscid in very wet weather but never gelatinous, inside solid, the shape equal with attenuate base, or fully equal and cylindric, or occasionally compressed, or tapering from the apex downward, straight or curved, 25–90 x 8–18–(40) mm. — *Context* of the pileus thick in the center, thin on margin, varying from almost white (though usually showing a slight brownish-orange tinge) to "buff pink," soft; of stipe "Congo pink" to subconcolorous with the pileus, the base mostly more or less yellow inside. *Odor* none to slight. *Taste* mild.

Spores (16)–18–21 x 5.8–6.5 μ, subcylindric-fusiform, smooth, melleous, grayish-melleous; *basidia* 4–spored, 40–55 x 11–12.8 μ; *cystidia* abundant, cylindric to cylindric-ventricose, or subcapitate, with narrowed base and rounded apex, incrusted or more rarely not incrusted, with or without granular contents, 95–150 x 12–18 μ, on sides and edges; *subhymenium*, *hymenopodium*, *lateral stratum*, and *mediostratum* as in *G. jamaicensis* (the subhymenium perhaps very slightly looser); *cuticle* of incrusted repent filamentous hyphae; *hyphae* without clamp connections.

Habitat: In mixed and pine woods under *Pinus* (species of the series *Insignes* and *Australes*), terrestrial, gregarious, fruiting from October to January.

Distribution: Maryland to South Carolina and west to Alabama and Tennessee, south to north Florida. In Florida rare, and observed only once in the western part of Alachua Co.

Material studied: **Fla.**: Near Seven-Mile-Church, 7 mi. west of Gainesville, January 8, 1940, *W. A. Murrill & J. R. Watson, det.* Murrill (*G. alachuanus*) (*ex* Herb. Erdman West, NY). — **N.J.**: Newfield, Oct. 10, 1887, on ground in pine woods, **Authentic** material of *P. pubescens* Ell. (NY). — **Md.**: South River near Annapolis, Oct. 6, 1919, *J. R. Morris, comm. H. A. Kelly* (*276*), *det.* L. C. C. Krieger (*Gomphidius spec.*) (MICH); Takoma Park, Oct. 12, 1918, *Kauffman* (*G. furcatus*). — **N. C.**: Chapel Hill, Oct. 1912, *W. B. Cobb 582* (NY). — **S. C.**: Society Hill, *Curtis 2855* (FH). — **Tenn.**: Ball Camp Pike, Nov. 1937, *Hesler & Sharp 10986, det.* A. H. Smith (*G. viscidus*) (MICH); Dec. 25, 1941, *L. R. Hesler* (*G. viscidus* f. *columbiana*) *14120* (MICH); near Clinton, Nov. 11, 1934, *L. R. Hesler 7792, det.* A. H. Smith (*G. vinicolor*) (FH, MICH). — **Ala.**: **type** of *G. alabamensis*, Auburn, Dec. 1900, *E. S. & F. S. Earle* (*2845*) (NY).

Earle published *G. alabamensis* in a key to the species of *Gomphidius*, but without a formal description. The characters given in the key do not determine the species as such, but notes with some of his specimens which he called *G. viscidus*, and the specimen which we consider the type of *G. alabamensis*, do not leave any doubt as to what Earle had in mind when he used the binomial *Gomphidius alabamensis*. The specimens of *G. furcatus* Peck, however, belong rather to *G. maculatus* than to this form, and we think, therefore, that Kauffman was wrong in identifying *G. alabamensis* with *G. furcatus*.

EXTRALIMITAL SPECIES

Gomphidius ochraceus Kauffm., Mycologia **17**(3): 119. 1925.

Gomphidius superiorensis Kauffm. & Smith, Papers Mich. Acad. Sci. Arts & Lett. **17**: 170. 1933. (a variety)

A polymorphous species, close to *G. rutilus*, not occurring in Florida.

Subgen. **Laricogomphus** Sing., (in press)

Characters of the subgenus: these are evident from the data in the key. Type species *G. maculatus* (Scop. *ex* Fr.) Fr. Not occurring in Florida.

Subgen. **Myxogomphus** Sing., (in press)

Characters of the subgenus: these are evident from the key. Type species *G. glutinosus* (Schaeff. *ex* Fr.) Fr.

Sect. **Macrosporus** Sing., (in press)

Characters of the section: these are evident from the key. Type species *G. glutinosus* (Schaeff. *ex* Fr.) Fr. This and the other species of this section, *viz. G. septentrionalis* Sing., *G. nigricans* Peck, *G. Smithii* Sing.,

G. subroseus Kauffm., *G. roseus* (Fr.) Karst. do not occur as far south as Florida.

Sect. **Microsporus** Sing., (in press)

Characters of the section: see key. Type species *G. oregonensis* Peck, a western species. Another species may occur in Europe, none in Florida.

SPECIES EXCLUDENDAE

Gomphidius foliiporus Murr.

This is *Phylloporus rhodoxanthus* ssp. *foliiporus* (Murr.) Sing.

Gomphidius rhodoxanthus (Schwein.) Sacc.

This is the American type of *Phylloporus rhodoxanthus* (Schw.) Bres.

PAXILLACEAE R. Maire (1902)

Characters of the family: pileus subtomentose to tomentose, sometimes viscid, small to large, the margin initially inrolled; hymenophore lamellose, but the lamellae very frequently connected by anastomosing veins and ridges, or the sides of the lamellae venose-rugose, more rarely the anastomoses broad and numerous and then the hymenophore resembles that of *Merulius*, arcuate, usually rather narrow, yellow, orange, or light tan to brown; spore print from nearly white to chamois or brownish; spores rather small to medium (3–11.5 μ long), smooth, ovoid, subglobose, ellipsoid or oblong-ellipsoid; cystidia present or absent; trama more or less bilateral; hyphae constantly with clamp connections; stipe very frequently eccentric to lateral or wanting; veil, said to be present in *Paxillus argentinus*, mostly none. Habitat: on earth or on wood, or on sawdust, rarer in the tropics but not entirely confined to extratropical regions, not forming mycorrhiza with specific flowering plants.

The Paxillaceae are closely related to the Boletaceae, especially the genus *Gyrodon*. Aside from the more individualized lamellae (even if they are connected by anastomoses), the more involute margin of young specimens, and the biological differences (*Gyrodon* and most of the Boletaceae being mycorrhizal fungi while the Paxillaceae do not seem to be dependent on symbiosis with specific forest trees, which does not mean that they will never and under no circumstances whatever form anything comparable with mycorrhiza-relationship), there are some minor differences that separate this family from *Gyrodon*. There is, for example, a slight but distinct difference in the chemical reactions (see the descriptions of the species). The greenish-yellow color of the hymenophores in *Gyrodon* is indicative of its close relationship with the Boletaceae. There is also the occurrence, in some species of *Gyrodon*, of autoxidation causing a blue discoloration of the hymenophore and the flesh. This latter reaction is, although not a constant feature of all *Gyrodon*, a character common to

many groups of the Boletaceae, while in the Paxillaceae this blue discoloration is constantly absent. There also appears to be some difference between the structure of the tube walls of *Gyrodon* and the trama of the lamellae in *Paxillus*. In the former, the mediostratum is somewhat denser and somewhat colored while the lateral stratum is distinctly divergent and hyaline in young material. In *Paxillus*, we found the lateral stratum of our sections definitely strongly interwoven, not clearly diverging, and of a rather different aspect when compared with the lateral stratum of the *Gyrodon* spp. — so different, indeed, that it is possible to consider it as non-homologous with the lateral stratum of the Boletaceae. Instead, the homology is with the hymenopodium of the Gomphidiaceae (see p. 529), which, however, may be difficult to prove, since the middle layer is always homogenous. In this family, as well as in the Gomphidiaceae, the structure of the hymenophore trama changes strongly while the carpophores mature.

I cannot see any good reason for splitting the genus *Paxillus* into several genera, merely on the, for the most part imaginary, differences in tramal structure. These species are otherwise so similar, exactly as the *Gomphidii*, that there is no doubt about their close natural affinities. This is confirmed by the chemical reactions registered by the author. One has only to compare the reactions of *Paxillus involutus* (see Ann. Myc. **40:** 58. 1942) with these of *P. panuoides* (see this paper, p. 542). *Crepidotus*, which has been compared with *Paxillus panuoides*, belongs in an entirely different sphere of affinities, being very close to *Ripartites* (which also has been considered as belonging to *Paxillus* by Quélet, Ricken, and others), and some other genera. *Phylloporus* is too close to certain Boletaceae, especially *Xerocomus*, to be retained in the Paxillaceae.

The Paxillaceae and the Gomphidiaceae are no doubt related, as may be expected of two lamellae-bearing families within the suborder Boletineae. Their tramal structure has some analogies. But biologically, in spore color, spore size, in chemical characters, and, most important, in clamp connections, they are consistently different. In many ways the Gomphidiaceae are comparable with the Strobilomycetaceae, and the Paxillaceae with the Boletaceae.

KEY TO THE GENERA, SECTIONS, AND SPECIES KNOWN TO THE AUTHOR

A. Spore print at least "chamois" (Ridgway), or somewhat deeper brownish; lamellae more or less anastomosing, at least in some portions of the hymenophore. Gen. *Paxillus*

B. Spores up to 7.5 μ large; cystidia none.

C. Stipe present, large, tomentose. Sect. *Atrotomentosi*

D. Trama of the lamellae lilac, in NH_4OH blue. *Paxillus polychrous*

D. Trama of the lamellae not as above. *Paxillus atrotomentosus*

C. Stipe present, and then lateral and short, or absent. Sect. *Panuoides*

E. Spores 3.8–6 x 3–4.5 μ. Odor none or not remarkable.
3. *Paxillus panuoides*

E. Spores 3–4 x 1.7–2 μ. Odor sometimes persistent, disagreeable.
Paxillus Curtisii

B. Most spores more than 7.5 μ long; cystidia present.
Sect. *Involuti*
Paxillus involutus

A. Spore print almost white (somewhat cream colored in thick layer); lamellae not or little anastomosing (though strongly forked), not venose on their sides.
Gen. *Hygrophoropsis*

F. Spores 4.8–8 x 2.7–4.8 μ; basidia 19–40 x 5–9.5 μ; pileus 35–85 mm. in diameter; stipe central or somewhat eccentric, very rarely strongly eccentric to lateral; habitat in coniferous woods or in mixed woods under conifers, on moss beds, or on coniferous wood, or on naked earth.
5. *Hygrophoropsis aurantiaca*

F. Spores 3.3–4.8 x 2.5–3.3 μ; basidia 16–20 x 3.7–6.8 μ; pileus up to 31 mm. in diameter; stipe strongly eccentric, lateral, or entirely wanting; habitat on sawdust, in hollow trunks (*e.g.* of *Nyssa silvatica*) but not on coniferous trunks, also occurring on old frondose logs in dense hammocks.
4. *Hygrophoropsis tapinia*

Paxillus Fr., Gen. Hymen., p. 8. 1836.
Ruthea Opat., Comm. Bol., Wiegm. Arch. **2:** 4. 1836.
Tapinia Karst., Hattsv., p. XXIII. 1879.
Tapinella Gilbert, Bolets, p. 67. 1931.
Rhymovis Rabenh., Kryptogamenfl. **1:** 453. 1844.
Paxillopsis Gilbert, Bolets, p. 86. 1931 (*nom. nud.*), *non* Lange, Fl. Agar. Dan. **4:** 47. 1939.
Plicaturella Murr., N. Amer. Flor. **9:** 172. 1910 (*sec.* Murrill).

Characters of the genus: these are evident in the key above. Type species, *P. involutus* (Batsch *ex* Fr.) Fr. The only species thus far observed in Florida is *P. panuoides*.

The nomenclatorial problem in the case of the genus *Paxillus* is a rather simple one. The genus *Paxillus* and the genus *Ruthea*, based on the same plants, were both proposed in 1836, and it certainly was a good idea to put *Paxillus* on the list of *nomina generica conservanda* as proposed by R. Maire to be accepted by the next Botanical Congress, since it may turn out that Opatowski's little-known name has a few days' priority over the generally accepted name *Paxillus*. Unfortunately, Gilbert's chapter about this family has caused many wrong citations and erroneous conceptions due to some inaccuracies in his book "Les Bolets." In his chapter on the "Histoire Taxonomique du Genre Paxillus" (p. 64–69), he says: "Persoon . . . a explicitement créé le genre *Rhymovis* sur le *P. involutus*, pour les seules espèces étroitement affines aux Bolets. Quoique puisse en dire Fries . . . , ce genre *Rhymovis* a la priorité. . . . Il est bien curieux de constater que Earle (1909) et Murrill ne l'aient pas reprise." Persoon, however, did not validly describe a genus *Rhymovis* though he may have had the intention of doing so in the future. "Si plures species," he

says (Mycologia Europaea **3:** 63), "inveniuntur, huic [*i.e. Agaricus involutus*] conformes, tunc ex iis genus distinctum efformari posset, *Rhymovis* [3] forte denominandum." It is inconceivable that anyone who has read this could possibly consider *Rhymoxis* as a published genus. It must be assumed that Earle and Murrill *did* read what Persoon said. They, therefore, knew that *Rhymovis* was not published before 1844 by Rabenhorst, *i.e.* eight years after Fries published *Paxillus*. Gilbert continues: "Berkeley (1836) crée lui aussi, sur *P. involutus*, un genre *Tapinia* qui sera repris comme sous-genre par Fries (1838) . . . Karsten (1879) . . . démembrait ce *Paxillus* (= *Tapinia*): *Paxillus* pour le *P. involutus* et ses affines, et *Tapinia* pour le *T. panuoides*. . . . Il est donc nécessaire de rejeter le terme générique *Tapinia*, d'ailleurs illégalement employé." If we check on Gilbert's "Histoire" again, it turns out that Berkeley in 1836 did not use *Tapinia* as a genus but as a subgenus. Karsten's *Tapinia*, therefore, is legal, though in my opinion not worthy of generic distinction. This whole situation was clear enough in the synonymy given in North American Flora **10**(3) : 146–147. 1917, and did not need to be "embrouillé" as late as 1931.

Sect. **Atrotomentosi** Sing. sect. nov.

Stipite praesente, vellereo; sporis parvulis; cystidiis nullis.

Characters of the section evident from the key above and the Latin diagnosis. Type species *P. atrotomentosus* (Batsch *ex* Fr.) Fr. Other species *P. polychrous* Sing. None of them found in Florida.

P. atrotomentosus is a well-known species, frequent in North America but not reaching Florida. Specimens from New Hampshire show the following chemical reactions, recorded here for comparison with *P. panuoides*. **NH_4OH** on the surface of the pileus coloring the tomentum and the pallid surface of the context, "dull lavender" to "slate purple" but leaving the cuticle proper unchanged brown in most cases (at least in old specimens); "dull lavender" to "slate purple" on the context of the pileus and the stipe but changing more slowly than on the surface of the pileus. — **KOH** on the surface of the pileus, a dark spot with a violet to lilac ring; on the context of the stipe, greenish; on the tomentum of the stipe, blackish. — **H_2SO_4** on the surface of the pileus where previously treated with KOH or NH_4OH becoming "yellow ocher," then "Buckthorn brown" in a few seconds, changing more slowly and more indistinctly at places where not previously treated with KOH or NH_4OH. — **$FeSO_4$** darker brown, and eventually greenish black on the pileus, and dull greenish gray on the context of the stipe, eventually blackish.

Sect. **Panuoides** Sing. sect. nov.

Pileo subsessili.

[3] "*Rhymovis*" was a printing error, and was corrected to *Rhymoxis* by Persoon in the Errata corrigenda of his *Mycologia Europaea*, v. 3, a fact which escaped Rabenhorst who is the only one who used Persoon's name.

Characters of the section evident from the key above and the Latin diagnosis. Type species *P. panuoides* (Fr. *ex* Fr.) Fr., the only species known in Florida. Another species is *P. Curtisii* Berk. *apud.* B. & C.

3. **Paxillus panuoides** (Fr. *ex* Fr.) Fr., Epicrisis, p. 318. 1938.

Agaricus panuoides Fr. *ex* Fr., Syst. Mycol. **1**:273. 1821.
Agaricus lamellirugis D. C. *ex* Secr., Mycogr. Suisse **2**: 457. 1833.
Agaricus croceolamellatus Let., Ann. Sci. Nat. sér. II. **3**: 94. 1835.
Cantharellus Dutrochetii Turpin *apud* Mont., Ann. Sci. Nat., sér. II, **5**: 342. 1836.
Rhymovis panuoides Rabenh., Kryptogamenfl. **1**: 453. 1844.
Paxillus rudis Berk. & Curt., Ann. Mag. Nat. Hist. ser. III. **4**: 296. 1859.
Paxillus ligneus Berk. & Curt., Jour. Linn. Soc. **9**: 423. 1867.
Crepidotus croceolamellatus Gill., Champ. Fr. Hym., p. 557. 1878.
Tapinia panuoides Karst., Hattsv., p. 452. 1879.
Paxillus acheruntius (Humb. *ex*) Schröter, Jahresb. Schles. Ges. für 1884, p. 300. 1885.
Paxillus lamellirugus Quél., Enchir., p. 93. 1886.
Paxillus ionipus Quél., Assoc. Fr. Avanc. Sci., Congrès d. Toulouse, p. 588. 1887.
Tapinia lamellosa (Sow. *ex*) Murr., N. Amer. Fl. **10**(3): 146. 1917.
Tapinella panuoides Gilbert, Bolets, p. 67. 1931.
?*Gomphus pezizoides* Pers., Mycol. Europ. **2**: 10. 1825.
?*Cantharellus olivaceus* Schw., Trans. Amer. Phil. Soc. ser. II. **4**: 296. 1832 (*sec.* Murrill).

Pileus dusky ochraceous to olive ochraceous, "cartridge buff," "cream buff," "chamois," "honey yellow," "Isabella color," "colonial buff," "deep colonial buff," sometimes the basal tomentum purplish-violet, the entire surface pubescent to more or less tomentose but usually glabrescent, sometimes rivulose, conchoid, or spathulate-substipitate, dimidiate or with a short, indistinct, concolorous, lateral stipe, 20–85–(100) mm. — *Hymenophore* concolorous or, especially when young and fresh, more yellow, reaching a color between "Naples yellow" and "mustard yellow," eventually more dirty tan, or "chamois" from the spore dust, easily separable from the context, lamellae decurrent or radiating from an eccentric point, rather narrow or narrow, crisp, anastomosing by veins, at least near the base of the pileus, and sometimes strongly anastomosing-lamellose and corrugate because of veins which transversely run down the sides of the lamellae, occasionally some forked without forming anastomoses, rather close to close; spore print "chamois." — *Context* cream color to whitish, soft, rather thin to thin, but sometimes gradually thickening to rather thick near the point of attachment; taste mild or very slightly bitterish; odor none, or not remarkable.

Spores 3.8–6 x 3–4.5 μ, mostly around 4.8 x 3.5 μ in America, 5.8 x 3.5 μ in Europe, melleous-pallid or pale melleous, smooth, thin-walled, ovoid-ellipsoid; *basidia* 19–26 x 4.5–6.2 μ; *cystidia* and *cheilocystidia* none; *trama* of the lamellae bilateral, the mediostratum and the lateral stratum equally dense or the former denser, especially farther away from the edge, splitting along the mediostratum on increase of pressure; mediostratum composed of subparallel-subinterwoven hyphae in young stages and near

the edges, of more truly interwoven hyphae in age and near the ground of the lamellae, but always with a distinct axillar orientation; lateral stratum mainly directed obliquely toward the subhymenium but increasingly interwoven, irregular, and even intermixed with age because of the presence of broad, sometimes clavate hyphae near the subhymenium; *cilia* of the marginal tomentum of the pileus formed by 4–5 μ thick, long hyphae; *hyphae* with clamp connections.

Chemical reactions: **KOH** on the surface of the pileus, olive; on lamellae and context, olive to dull deep yellow; NH_3–vapors on the surface of the pileus, strongly lilaceous-drab, livid; H_2SO_4 on the surface of the pileus, dull, deep yellow, little reaction elsewhere; $FeSO_4$ on context slightly olive.

Habitat: On coniferous wood, on trunks and stumps in the forests as well as on structural wood in houses, on bridges, in mines, etc. where it is apt to develop fertile though mostly resupinate fruiting bodies in perfect darkness; preferring pine. Fruiting in summer to late fall if growing in the open in the northern states, elsewhere also found fruiting in winter and spring. Usually gregarious, frequently cespitose.

Distribution: Nearly a cosmopolite, but rarer or partly absent in the tropics. Known from North, Central and South America, Europe, Asia, Africa, and Australia. In Florida not common.

Material studied: **Fla.:** Alachua Co., Cary Forest, Nov. 1938, *Erdman West & W. A. Murrill, det.* Murrill, *F 17708* (FLAS).—**N. H.:** August 1860, *Blake, det.* Curtis *740* (FH).—**Mass.:** Harvard, on coniferous wood, July 1944, *Harrie Dadmun & R. Singer* (*det.* R. Singer) (FH); *Murray, Sprague* (*581*) (FH); type of *P. ligneus* B. & C. *Murray, Sprague* (*1149*) (FH); Floating Bridge, Lynn, August 1913, *E. B. Blackford* (FH); Arlington, Oct. 1907, *Piguet, det.* Farlow (FH).—**Conn.:** type of *P. hirtus* B. & C., *Wright 234* (FH).—**N. Y.:** Enfield Gorge, Sept. 1903, *C. H. Kauffman* (FH).—**S. C.:** Santee Canal, *Ravenel* (*1038*) (FH).—**Ga.:** NortheastGa. near Tallulah Falls, Tannery Brook, August 1901, *A. B. Seymour, det.* Farlow (FH).—**Tenn.:** Great Smoky Mts., Greenbrier, July 1939, *L. R. Hesler* (FH); Grassy Patch, July 1940, *A. J. Sharp, det.* L. R. Hesler (FH).—**Ala.:** "Alabama superioris" Dec. 1855, *Peters* (*925*) (FH).—**Ore.:** Wygand State Park, Hood River Co. Oct. 1937, *W. B. Cooke* (*9675*).—**Cal.:** Berkeley, February 1933 (FH).—**Mexico:** *Botteri, det.* Curtis (as *P. ligneus*) (2) (FH).—**Brazil:** São Leopoldo, 1932, *Rick* (FH).—**Sweden:** Upsala, 1853, *E. P. Fries* (FH).—**U.S.S.R.** (former Finland): Kellomäki, Sept. 1940, *R. Singer 5–789* (LE).

The European plant usually has slightly larger spores, but this character is by no means constant. Excellent colored figures of this have been published, best of all is that in Lange, Flor. Agar. Dan. **4:** pl. 134, *fig. B.* Elrod and Blanchard's photomicrograph (Mycologia **31:** 697. *fig. 1, D.* 1939) of the gill trama gives an idea of the structure of a not quite young though not very old specimen, but few details are visible. Josserand (Bull. Soc. Myc. Fr. **48**(2):112. *pl. 13, fig. 3.* 1932) published a better figure, showing exactly what we have seen and described above.

EXTRALIMITAL SPECIES

Paxillus Curtisii Berk. *apud* Berk. & Curt., Ann. Mag. Nat. Hist. ser. II. **12:** 423. 1853.

Paxillus corrugatus Atk., Stud. Amer. Fung., p. 170. 1900.

This species has smaller spores than *P. panuoides*, as is shown by examination of the type (on pine wood in Georgia), collected by Ravenel in September 1848, # 853, preserved at the Farlow Herbarium. In fact these spores are the smallest known in the Boletineae. Since this species occurs from New England to Georgia, it is possible that it will be discovered in north Florida.

Sect. **Involuti** Sing. sect. nov.

Pileo lateraliter vel excentrice vel subcentraliter stipitato; stipite glabro; sporis volumine mediocri gaudentibus; cystidiis praesentibus.

Characters of the section: see the key p. 539, and the above Latin diagnosis.

Paxillus involutus (Batsch *ex* Fr.) Fr. Epicrisis, p. 317. 1838.

This common and widely distributed species is remarkable for its absence in Florida. It occurs in Uruguay where it has been collected by Herter, determined as *Paxillus argentinus*, which strongly differs in having a veil. The trama of these specimens is divided into an intermixed-interwoven hymenopodium, and a subregular mediostratum or rather trama proper, consisting of brownish, 3.5–9 μ broad hyphae, while in the hymenopodium the hyphae are hyaline to brownish and still more variable in diameter; all hyphae with clamp connections; spores 8–11.5–(13) x 5–7.5 μ, the wall occasionally up to 1 μ thick; basidia 4-spored, about 31 x 7.8–9.8 μ; cystidia hyaline to brownish, versiform, 34–65 x 13–20 μ; hyphae of the cuticular layer of the pileus repent, long-cylindric. For the chemical reactions of European specimens, see Ann. Myc. **40:** 58. 1942.

SPECIES EXCLUDENDAE

Paxillus miniatus Rick, Broteria **5:** 19. 1906.

The type of this species does not exist in Brazil; authentic material kindly sent by J. Rick does not fit in the original diagnosis, and is a species of the Lentineae with smooth, hyaline spores. We therefore consider *P. miniatus* as a dubious species, and propose *P. russuloides* Petch as the type species of the genus *Phyllobolites* Sing. *P. lateritius* is also thought to belong in *Phyllobolites*.

Paxillus pubescens Ellis, see under *Gomphidius rutilus* ssp. *alabamensis*.

Paxillus pinguis Hook. fil. *apud* Berk., Hook. Journ. Bot. **3:** 41. 1851.

This is, as is shown by the unpublished colored figure of Hooker (FH), one of the subspecies of *Phylloporus rhodoxanthus*, and so are certainly *Paxillus flavidus* Berk., Lond. Journ. Bot. **6:** 315. 1847, *Paxillus rhodoxanthus* (Schw.) Ricken, Blätterpilze. **1:** 95. 1911, *Paxillus Tammii* Pat., Tab. Anal. **4:** 161. 1885, *Paxillus Pelletieri* (Lév.) Velen., Česk. Houb., p. 356. 1920, and *Paxillus paradoxus* (Kalchbr.) Cooke, Grevillea **5:** 6. 1876. *Paxillus sulphureus* Berk. is most probably another species of *Phylloporus*.

Paxillus prunulus (Scop. *ex* Fr.) Quél., Enchir., p. 92. 1886.

See *Clitopilus prunulus* Jugasporaceae, p. 551 of this paper.

Paxillus reniformis Berk. & Rav. *apud* Berk. & Curt., Ann. Mag. Nat. Hist. ser. II. **12:** 424. 1853.

This species described from North Carolina has been compared with *Paxillus panuoides* by Murrill, N. Amer. Fl. **10**(3): 146. 1917. However, the type (FH) has verrucosely punctate spores of 8.3–10.2 x 5.5–6.5 μ, and all the main characters of a *Crepidotus*. The combination **Crepidotus reniformis** (B. & R.) Sing. comb. nov. is proposed. *C. versutus* Peck is probably the same species.

Hygrophoropsis R. Maire *apud* Martin-Sans, L'Empoisonnement, p. 99. 1929.

Cantharellus subgen. *Hygrophoropsis* Schröter in Cohn, Krypt. Fl. Schles. **3**(1): 511. 1889.

Merulius S.F. Gray, Nat. Arr. Brit. Pl. **1:** 636. 1821 (*non* Fries).

Characters of the genus: see key, p. 539. Type species, *Hygrophoropsis aurantiaca* (Wulf. *ex* Fr.) Maire *apud* Martin-Sans [*Cantharellus aurantiacus* (Wulf.) *ex* Fr.]

The species entering this genus were formerly considered to belong in *Cantharellus*, but since they are fundamentally different in many regards from the type species of that genus, they were transferred by Studer, Maire, and others to *Clitocybe*. The writer formerly agreed with this point of view though *Hygrophoropsis* did not show close relationship with any group of *Clitocybe*. It appears that the characters in common with *Paxillus* are much more striking than the ones that suggested the comparison of *Hygrophoropsis* with *Clitocybe*. The soft context is typical for the Boletineae, and the tramal structure is strongly reminiscent of *Paxillus* and *Clitopilus*. The small, slightly yellowish spores are similar to these of *Paxillus panuoides*. The discovery of a second species, *H. tapinia*, with smaller spores and an external appearance frankly suggesting *Paxillus Curtisii* but never met with in *Clitocybe*, makes the affinity between *Hygrophoropsis* and *Paxillus* an established fact.

4. **Hygrophoropsis tapinia** Sing. spec. nov.

Pileo pallide aurantiaco, admodum excentrico vel astipitato, tomentoso, infundibuliformi-irregulari, carnoso atque tenui, usque ad 35 mm. lato; lamellis aurantiacis,

immutabilibus, furcatis, haud anastomosantibus nec corrugatis, acie obtusa instructis, angustis, descendentibus vel arcuate distincte profundeque decurrentibus; sporis in cumulo albidis, sub microscopio hyalinis vel pallide luteolis, 3.3–4.8 x 2.5–3.3 μ; basidiis 16–20 x 3.7–6.8 μ; cystidiis nullis; hyphis fibuligeris; stipite pumilo vel nullo, concolori; carne pallidiore, immutabili, molli, inodora. Habitatio: In truncis cavis, ad sarmenta in dumetis, etc., Septembri et Octobri mensibus, Florida, U.S.A.

Pileus "pale orange yellow," very eccentric to astipitate, tomentose, infundibuliform or irregular, fleshy but rather thin, up to 35 mm. broad. — *Hymenophore* "capucine orange," becoming brownish orange, unchanging on drying and on injury, strongly forking but not anastomosing nor corrugate, smooth with blunt edges, narrow, decurrent; spore print white or whitish on white paper in thin layer. — *Stipe* small, concolorous, or wanting. — *Context* paler than the surface, unchanging, soft, inodorous.

Spores hyaline to pale yellow under the microscope, 3.3–4.8 x 2.5–3.3 μ; *basidia* mostly 4–spored, 16–20 x 3.7–6.8 μ; *sterile bodies* in the hymenium not infrequent (aborted basidia?), extremely variable in shape, usually numerous on edge; typical *cystidia* absent; *trama* consisting of hyaline, thick (0.7μ) or thin-walled, often slightly gelatinized hyphae, bilateral with more parallel-subinterwoven hyphae in the axillarly arranged mediostratum (respectively trama proper), and with more irregularly arranged but mostly straight hyphae in the accompanying layers (lateral stratum or hymenopodium); *clamp connections* numerous.

Habitat: On dead trunks of frondose trees and on sawdust in dense hammocks, never under or on conifers. September and October.

Distribution: South Florida.

Material studied: **Fla.**: Dade Co., Simpson Park, Miami, on sawdust in dense tropical hammock vegetation, October 1942, *R. Singer F 1037* (FH); Brickell's Hammock, Miami, on a dead trunk in tropical hammock, October 1942, *R. Singer, F 1273* (FH).

This species is very close to *Hygrophoropsis aurantiaca* from which it is distinguished mainly by the smaller spores and the habit of fruiting which suggest *Paxillus Curtisii*. The description of a British species, *Paxillus Fagi*, may suggest to some our Florida species, but it is too poorly characterized and moreover the surface is said to be pallid. *Paxillus aurantiacus* Ellis probably belongs in this group but it reminds one rather of *Hygrophoropsis aurantiaca* than of *H. tapinia*.

5. **Hygrophoropsis aurantiaca** (Wulfen *ex* Fr.) R. Maire *apud* Martin-Sans, L'Empoisonnement p. 99. 1929.

Cantharellus aurantiacus Fr., Syst. Myc. **1:** 318. 1821.
Merulius aurantiacus Persoon *ex* S. F. Gray, Nat. Arr. Brit. Pl. **1:** 636. 1821.
Cantharellus Ravenelii Berk. & Curt., Ann. Mag. Nat. Hist. ser. II. **12:** 425. 1853.
Clitocybe aurantiaca Studer, Beiblatt z. Hedwigia **39:**(7). 1900.
Chanterel alectorolophoides (Schaeff. *ex*) Murrill, N. Amer. Flora **9**(3): 169. 1910.

Var. **typica**

The type variety is a common species in the northern states of this country, in Canada, in Europe, especially in the northern and central part of that continent, and in Asia. I have collected typical specimens in all these regions but not farther south than the Caucasus Mts. in Asia. D. H. Linder has collected good specimens in Virginia, U.S.A., as did L. R. Hesler in Tennessee, and Ravenel collected the type of *Cantharellus Ravenelii* B. & C. in South Carolina. This is definitely the most southerly place where this species has been found in this hemisphere. The type is in rather good condition, and appears to belong here, as suggested by Murrill. The spores of the type variety are 4.8–8 x 2.7–4.8 μ, ellipsoid to cylindric or rarely reniform, thin-walled, or somewhat thick-walled, hyaline to slightly yellowish-hyaline; basidia 19–40 x 5–9.5 μ; cystidia none, or rare, but sometimes some aborted basidia present; the trama consists of a mediostratum (trama proper) with distinctly subparallel-interwoven thicker-walled hyphae which are more loosely arranged than in the hymenopodium; the latter strongly irregular, the hyphae running in all directions, many of them obliquely toward the subhymenium; the hyphae making up the hymenopodium are denser and slightly thinner and also have somewhat thinner walls than the hyphae of the mediostratum; the latter is distinctly continued above the dorsal end of the lamellae just below the context of the pileus as can be observed in most Boletineae. Paler to partially white carpophores are not infrequently observed in northern Europe, and have been described under various varietal names. For a complete description of this species, see Ann. Myc. **41**: 22. 1943, under *Clitocybe aurantiaca*. The type variety has not been observed as far south as Florida. We have observed only a single specimen of what we think is a dwarf form or a smaller race of this species since it is regularly stipitate and has the spores of the general measurements of this species. However, it was found on frondose trunk in low hammock, far from any conifers and this makes it more remarkable.

Var. **nana** Sing. var. nov.

Carpophoris minusculis, gracillimis et habitatione in truncis cavis arborum frondosarum in silva palustri subtropicali a typo differt.

Pileus brown, velutinous-tomentose, dry, convex, 6 mm. broad; margin smooth, initially involute. — *Lamellae* reddish orange, orange, narrow, forked, subobtuse at the edge, decidedly decurrent, descendant or arcuate, rather close; spore print not obtained. — *Stipe* dirty orange brownish, subvelutinous, solid, subequal, soft, 9 x 1 mm. — *Context* subconcolorous with the surfaces, soft, mild to the taste, inodorous.

Spores hyaline, 6–8 x 3.5–3.7μ, ellipsoid to subcylindric, smooth, nonamyloid; *basidia* 20–30 x 5–7.7 μ; *cystidia* none seen; *trama* as described in the type; *tomentum of the pileus* consisting of loosely interwoven hyphae, some of them slightly rough (from gelatinous matter), filamentous-cylindric, hyaline, 3–7 μ in diameter; all *hyphae* with clamp connections.

Chemical reactions: KOH, NH_4OH, and $FeSO_4$: little reaction.

Habitat: In the hollow trunk of living *Nyssa sylvatica*, in low hammock vegetation, far from conifers. Solitary in summer.

Distribution: Known only from the type locality.

Material studied: **Fla.:** Highlands Co., Highlands Hammock State Park, Sept. 1942. *R. Singer, F 640, type* (FH).

SPECIES INCERTAE SEDIS

Hygrophoropsis albida (Fr.) R. Maire, Publ. Inst. Botàn. **3**(4): 58. 1937.
Cantharellus albidus Fr., Syst. Mycol. **1:** 319. 1821.

This species has been described from Sweden. I have a few times collected specimens which I used to attribute to it, but since I have not recently restudied any of these, I hesitate to refer them here, for the available dried material is not well enough preserved to allow more detailed anatomical studies. *Cantharellus albidus* (*Hygrophoropsis albida*) does not occur in Florida. Maire thinks it belongs in this genus. He lists it in the family Leptotaceae, but the type genus of that family, *Leptotus*, belongs in the Cyphellineae, and has nothing in common with *Hygrophoropsis*, as a special study of the Leptotaceae showed (see R. Singer, The *Laschia*-complex. Lloydia **8:** 188. 1945.)

JUGASPORACEAE (Kühner *ut trib.*) Sing. (1936)

Characters of the family: pileus subglabrous to sericeous, smooth or more rarely venose, not viscid or scarcely viscid, small or rather large, the margin initially frequently involute, the color as in the whole carpophore usually pallid, white, more rarely light gray; hymenophore lamellose, lamellae decurrent if there is a stipe; spore print pink; context with more or less distinct farinaceous odor, more rarely subinodorous; stipe central eccentric, lateral or absent; veil none; spores hyaline to pale stramineous under the microscope, with 5–10 longitudinal ridges or veins or blunt angles formed by flattened stripes running from the hilar end to the apex, without germinative pore, thin-walled, the wall easily collapsing and the folds thus formed sometimes resembling additional ridges, young spores more smooth and rounded, ovoid, ellipsoid, fusoid, asymmetrical; cystidia none; hyphae of the cuticle and the surface of the stipe (if present) repent; trama consisting of a mediostratum of interwoven to subirregular hyphae with a generally axillar arrangement, and becoming more parallel-regular when seen at a point closer to the edge, conspicuously intermixed near the ground (dorsal part) of the lamellae, looser in the mediostratum, and the hyphae thicker than in the lateral stratum (hymenopodium) where some hyphae run obliquely toward the hymenium. The hyphae generally are irregularly interlaced, and in neither the mediostratum nor the lateral stratum are they as loosely arranged as in *Boletus*. The species are homothallic (*sec.* Kühner & Vandendries). All hyphae are without clamp connections.

Habitat: On the soil and on various organic material, wood, dung, dead Cormophyta, etc.

The Jugasporaceae form a very natural family. They have important characters in common with the Paxillaceae: the general appearance and biology, the shape and size of the spores, the structure of the trama (though the bilateral character of the latter is still less evident in the Jugasporaceae than it is in the Paxillaceae), the soft context, the occurrence of poroid hymenophores in aborted carpophores, the absence of cystidia (if *Paxillus involutus* is exempted), and the initially involute margin. On the other hand, it cannot be denied that there is a slight analogy with the Rhodogoniosporaceae, in the color of the spores in prints, the odor, and the frequent occurrence of pigmentless species. It is a fact that the sessile as well as the smaller stipitate forms of *Rhodophyllus* and *Clitopilus* are hard to distinguish if one has to rely on macroscopical characters only. It is just as true that some *Rhodophylli* with very rounded angles on the spores are equally hard to distinguish from the Tricholomataceae, such as *Rhodocybe* (cf. Lloydia **5**(2): 110. 1942). Lange relates *Clitopilus prunulus* to the Paxilli by putting it in a neighboring genus *Paxillopsis* Lange, but this latter genus is complex, containing all kinds of atypical Paxilli, including even *Rhodopaxillus*. Ricken, following Quélet, made *Clitopilus* a straight synonym of *Paxillus*, but his generic conception of *Paxillus* was still very broad, evidently under the influence of Quélet and Fries. Lundell, in *Fungi Exsiccati Suecici* #137 says: "Modern authors have placed it in the genus *Paxillus*. Lange justly eliminates *Clitopilus* altogether, and placed the smooth-spored species with *Paxillus*, and the angular-spored ones with *Eccilia*." Since Lundell understands *Paxillus* in a somewhat restricted sense, probably in approximately the same way as we do, his classification of *Clitopilus prunulus* within a restricted genus *Paxillus* goes much farther than I would go considering the differences between *Clitopilus* and *Paxillus*, especially in the spore color and clamp connections. Fayod (1889) comes closest to the point of view expressed in my papers since 1936. He has the following arrangement: Series D: Tribe 25 Goniosporés (the genera now considered as *Rhodophyllus*); Tribe 26 Paxillés (the genera here combined in the genus *Paxillus* and the genus *Gomphidius*); Tribe 27 Fusisporés (the genera here combined in *Clitopilus*). Fayod also admits the affinity of the Paxillés with certain boletes, but so did Opatowski in 1836.

The position of the Jugasporaceae in the classification of the Agaricales is one of the most difficult problems in spite of the large number of facts now available. If the similarity with the Rhodogoniosporaceae and *Rhodocybe* (in the first case the external similarity, in the latter case the similarity of the spores [4]) is considered to show affinity, we arrive at the

[4] The spores of *Rhodocybe alutacea* Sing. *ined.*, a species closely related to **R. truncata** (Fr.) Sing. comb. nov. ssp. *subvermicularis* (Maire) Sing. (*Rhodopaxillus truncatus* (Fr.) Maire var. *subvermicularis* Maire from North Africa, are at the same time warty because of thickenings of the wall, and when seen from above, obtusely applanate forming a hexagon. This latter character reminds one strongly of *Clitopilus*,

alternative solutions of this problem: either the Jugasporaceae are at the same time related with the Rhodogoniosporaceae (*Rhodophyllus*, *Rhodocybe*) on one hand, and the Paxillaceae on the other hand, or the Rhodogoniosporaceae and *Rhodocybe* would better be added to the Boletineae in the larger sense, or the Jugasporaceae could be combined with the family Rhodogoniosporaceae (*Rhodophyllus*, *Rhodocybe*). In view of the strong arguments in favor of an affinity with the Paxillaceae, and the plurality of possibilities suggested by the similarities with the Rhodogoniosporaceae and *Rhodocybe*, we think it best to leave the Jugasporaceae within the Boletineae at present, and wait for new facts to be found that might throw more light on the presumed affinity with other pink-spored agarics. It may well be that this affinity is not more than a certain coincidental similarity in spore shape.

Since the type concept, now obligatory in nomenclature, excludes the elimination of *Clitopilus*, and also its reestablishment in a modified sense as formerly advocated by R. Heim and myself, I cannot but follow the example of Konrad and Maublanc, R. Maire, Josserand, and others who use the genus *Clitopilus* in the way it is used in the present paper. The question of whether the smaller species should be kept in a separate genus (*Octojuga* Fay.), or combined with *Clitopilus*, is, as I have emphasized on several occasions, a question of the definition of the word genus. As it seemed before the entrance of certain intermediate species into the taxonomic picture of this family, the larger and the smaller species were well separated by several correlated characters, i.e. the striation and the size of the spores, the general appearance, and the habitat. Since then, however, it has turned out that minute species like *Omphalia Giovanellae* Bres. (see Mycologia **34:** 66. 1942) and *Omphalia scyphoides* Fr. belong here, species with central or eccentric stipe like *Clitopilus prunulus*, and also growing on the soil. The difference in the spores does not seem to be so important now since I have studied many species and specimens, and find that only the length of the spores is consistently though slightly different in the two groups. Two Indo-Chinese species, one of them (*C. crispus*) very similar to *C. prunulus*, have strongly 8–10–ribbed spores instead of 6–ribbed ones, and besides the spores are shorter than in *C. prunulus*. I therefore do not think that the differences as they appear now are sufficient for the establishment of two genera within the family Jugasporaceae, and, like Josserand (Bull. Soc. Myc. Fr. **53:** 209–213. 1937), I admit (*l.c.*) only one genus *Clitopilus*.

The longitudinal striation of the spores of the Jugasporaceae cannot be identified with the ridges of the spores in *Boletellus*. In the latter case, the optical section through the short axis of the spore shows terete spores with

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and as a matter of fact, Kühner has recently stated that in his opinion *Clitopilus prunulus* is related to certain species of *Rhodopaxillus* as he calls the clampless species which we refer to *Rhodocybe* in spite of the lack of pseudocystidia, *e.g. Rhodocybe fallax* (Quél.) Sing. Syn: *Rhodopaxillus fallax* (Quél.) R. Maire. See Bull. Soc. Linn. Lyon, Sept. et Oct. 1945, no. 7–8.

the veins or lamellose ridges projecting like thorns or wings, while in the Jugasporaceae we have a regular hexagon (with the angles slightly protracted or mucronate in *Clitopilus prunulus*) or heptagon, octagon, etc. In the latter case, the angles often are so obtuse that the striation of the spores is extremely difficult to observe, and only the outline of an optical section with the longer axis vertically directed towards the objective reveals the character of the spore. This character may also be obscured by the fact that young spores are more round in this position, and some do not seem ever to reach the striate stage. This is the case with *Clitopilus scyphoides*, and, to a lesser degree, *C. Passeckerianus*. But even then the color of the spore print should easily exclude the genus *Omphalia*, and the lack of clamp connections should exclude *Clitocybe*, *Dochmiopus*, etc.

Clitopilus (Fr.) Quél., Champ. Jura p. 120. 1872, *sensu* Patouillard, Hym. Eur., p. 113. 1887.
Agaricus trib. *Mouceron* Fr., Syst. Myc. **1:** 193. 1821.
Agaricus trib. *Clitopilus* Fr., Epicrisis, p. 148. 1836, *non* Syst. Mycol.
Hexajuga Fayod, Ann. Sci. Nat., sér. VII. **9:** 389. 1889.
Octojuga Fayod, Ann. Sci. Nat., sér. VII. **9:** 390. 1889.

Characters of the genus: they are the same as for the family. The type species is *Clitopilus prunulus* (Scop. *ex* Fr.) Quél. (*Agaricus prunulus* Fr.)

KEY TO THE SECTIONS AND SPECIES KNOWN TO THE AUTHOR

A. Carpophore medium to rather large, pileus 30–130 mm. broad, fleshy, with the external appearance of a larger *Clitocybe*, or *Paxillus involutus*; spores with 6 longitudinal furrows between 6 longitudinal folds or ridges, and therefore three-striate when seen in profile, (7)–10–14 μ long: growing on the soil.
Sect. *Prunuli*
6. *Clitopilus prunulus*

A. Carpophore smaller than indicated above, or spores smaller; spores either ridged as above, or seemingly smooth but appearing polygonal when seen from one end (with the longer diameter vertically directed toward the objective), 5.5–11.5 μ long, ridges or angles variable in number, usually more than 6, often up to 10; growing on the soil (mostly sand), or on various debris, rotting or rotten wood, manure, etc.

B. Stipe present, constantly persistent. Sect. *Scyphoides*

C. On horse manure in mushroom cellars; stipe very small, less than 3 mm. long. *Clitopilus Passeckerianus*

C. Not on manure, only in the open; stipe usually larger.

D. Pileus gray. 7. *Clitopilus Giovanellae*

D. Pileus white.

E. Spores with scarcely projecting ridges or folds, merely angular when seen from one end. 8. *Clitopilus scyphoides*

E. Spores with strongly (0.3–0.4 μ) projecting longitudinal ridges or folds.

F. Pileus fleshy with crenate margin. *Clitopilus crispus*

F. Pileus thin with smooth, entire margin.
Clitopilus orcelloides

B. Stipe absent, or spurious, or disappearing with age, or inconstant. Sect. *Pleurotelloides*

G. On horse manure, in white-mushroom cellars. (Rare astipitate form of *Clitopilus Passeckerianus*)

G. On substrata other than manure.

H. Pileus rugose-venose; growing on the wood of evergreen trees in tropical hammock. 9. *Clitopilus venososulcatus*

H. Pileus smooth, or transparently striate. 10. *Clitopilus pleurotelloides*

Sect. **Prunuli** (Quél. ut sectio subgeneris *Orcellae* generis *Paxilli*, Ench., p. 92, 1886) *em.*

Carpophoris mediocribus vel majusculis, carnosis, distincte stipitatis; sporis 6 rugis longitudinalibus instructis, 10–14 μ longis. Ad terram.

Characters of the section: they are evident from the key and the Latin diagnosis above. Type species as in the genus *Clitopilus*.

6. **Clitopilus prunulus** (Scop. *ex* Fr.) Quél., Champ. Jura, p. 120. 1872.

Agaricus prunulus Scop. *ex* Fr., Syst. Mycol. **1:** 193. 1821.
Agaricus orcellus Bull. *ex* Fr., Syst. Mycol. **1:** 180. 1821.
Clitopilus orcellus Quél., Champ. Jura, p. 120. 1872.
Paxillus prunulus Quél., Enchir., p. 92. 1886.
Paxillus prunulus var. *orcella* Quél., Enchir., p. 92. 1886.
Hexajuga prunulus Fayod, Ann. Sci. Nat., sér. VII. **9:** 289. 1889.
Rhodosporus prunulus Schröter, *in* Cohn, Krypt.-Fl. Schles. **3**(1): 618. 1889.
Pleuropus prunulus Murr. N. Amer. Fl. **10**(2): 104. 1917.
Pleuropus obesus Murr., N. Amer. Fl. **10**(2): 105. 1917.
Paxillopsis prunulus Lange, Flora Agar. Dan. **4:** 48. 1939.

Pileus whitish, whitish-gray, whitish-cream, sometimes with spots, dots, or zones, sometimes scarcely subviscid during rains, but usually quite dry, mostly finely velutinous or innately mealy, convex but very soon flatter and depressed though usually very irregular, with involute, eventually irregularly-lobed margin, and obtuse, rarely indistinctly umbonate disc, smooth, 30–130 mm. broad. — *Hymenophore* white or whitish, then pale incarnate, easily separable from the context of the pileus, lamellae frequently not straight, moderately close to close, rather narrow or narrow (up to 4 mm. broad), deeply decurrent; spore print "fawn color." — *Stipe* white or concolorous with the pileus, slightly fibrillosely striate, glabrous or subglabrous, often with tomentose base, naked, versiform, solid, but softer inside, 26–50 x 6–21 mm. — *Context* white, soft, with the consistency of a bolete; taste mild, farinaceous; odor strong, farinaceous (of fresh flour, or flowers of *Berberis vulgaris*).

Spores elongate-ovoid to mostly subfusoid, with distinct suprahilar depression, with (5)–6–(7) longitudinal brims or edges which usually are more or less projecting, forming low ridges or folds with furrows running between them, the angular outline well-marked in an optical section with the long diameter of the spore vertically directed towards the objective (use chloral hydrate as medium), hyaline to hyaline-stramineous, asymi-

metric, (7)–10–14 x 5–6 μ, most frequently 10.5–12 x 5–5.8 μ; *basidia* 4–spored, 30–36 x 8.3–9.8 μ; *cystidia* and *cheilocystidia* none; *trama* of the lamellae intermixed-subbilateral, the mediostratum differing from the lateral stratum respectively the hymenopodium [5] in consisting of large, irregularly arranged elements in the basal (dorsal) portion of the lamellae, and generally in being less densely interlaced, and much thicker; toward the edge of the lamellae these differences become less distinct, the mediostratum becoming more regular and its elements more elongate and narrow, and even the hymenopodium becoming slightly less interlaced, its hyphae showing a slight but indistinct tendency to diverge toward the hymenium, 5.5–6μ in diameter; hyphae of the *cuticular* layer of the pileus repent, cylindric-filamentous; all *hyphae* consistently without clamp connections.

Chemical reactions: **NH_4OH,** yellowish-brown-vitreous. — **$FeSO_4$,** no reaction. — **Guaiacol** reacting only in the base of the stipe, and even there weakly and slowly. — **Methylparamidophenol,** negative to weak, or moderate reaction in stipe, no reaction or only a weak one on the pileus, the edges of the lamellae usually becoming distinctly deep umbrinous, in young specimens the surface of the pileus and the edges of the lamellae becoming distinctly deep violet but the rest of the carpophore remaining negative.

Habitat: In open woods and gardens, in meadows near isolated trees of all kinds, always on the soil, on sandy earth as well as on limestone; fruiting from May to November, usually in small groups.

Distribution: Europe, Caucasus, North Africa, North America south to Florida. In Florida known only from well-watered lawns in north Florida.

Material studied: **Fla.:** Alachua Co. Gainesville, some collections by *W. A. Murrill* (*Pleuropus obesus*) (FLAS); by *R. Singer F 1867, F 1867a* (FH). — **N. H.:** Chocorua, August 1904, *Farlow* (FH). — **Mass.:** Canton, August 1925, *D. H. Linder* (*C. orcellus*) (FH); Wakefield, August 1943, *R. Singer* (FH). — **N. Y.:** Newcomb Co., Mt. Goodenow, September 1941, *R. Singer* (FH). — **Ia.:** Iowa City, September 1936, *G. W. Martin* (FH). — **Tenn.:** Highlands, August 1936, *L. R. Hesler & A. J. Sharp* (FH). — **Canada: N. B.,** October 1903, *det.* Farlow (FH). — **U.S.S.R.:** Moscow region, Mikhailowskoe, June 1896, *Buchholz* (FH); Leningrad region, near Ryabovo, August 1938, *R. Singer* (*Hexajuga prunulus*) (LE). — **Spain:** Catalonia, Salardú, June to October 1934, *R. Singer* (BA). — Numerous collections of the fresh fungus in Czechoslovakia, Austria, Bavaria, and France, and abundant dried material from all European countries in the European herbaria. — Asiatic part of the **U.S.S.R.,** Caucasus, Abkhazia, Saken, August 1928, *R. Singer*; Caucasus, Guzeripl, August 1935, *L. N. Vassilieva* (KAZ).

This is an easily identified species, and one of the less-known but excellent edible mushrooms. *Clitopilus orcellus* is only an insignificant form of this species. Its occurrence in Gainesville, south of the 30th parallel, probably marks the southernmost limit of the species.

[5] What I call the hymenopodium, has been described by others as the subhymenium, *e.g.* by R. Maire for *Clitopilus cretaceus* Mre. (See also p. 538 and 547 of this paper.)

Sect. **Scyphoides** Sing. sect. nov.

Carpophoris vix mediocribus, aut sporis minoribus quam 10 μ et tunc carpophoris nonnunquam mediocribus vel submajusculis, constanter distincte stipitatis.

Characters of the section: compare the key p. 550, and the above Latin diagnosis. The type species is *Clitopilus scyphoides* (Fr.) Sing., more exactly var. *typicus* fa. *typicus*, as defined below, p. 554.

7. **Clitopilus Giovanellae** (Bres.) Sing., Mycologia **34:** 66. 1942.
Omphalia Giovanellae Bres., Fung. Trid. **1:** 9, *pl. 5, fig. 2.* 1881.

Pileus gray, sometimes somewhat shining, sericeous, smooth, but often subrugulose on the margin, and also slightly transparently striate at the extreme margin when wet and quite mature, not viscid, convex with a deep umbilicus in the center from the beginning, eventually becoming flatter to infundibuliform, 6–8 mm. broad (5–14 mm. according to Bresadola). — *Hymenophore* pale gray, easy to separate from the context of the pileus, lamellae very thin and slender, deep decurrent, arcuate, subclose to close, narrow; spore print pinkish. — *Stipe* grayish-white to gray, somewhat silky, central, or sometimes somewhat eccentric, subequal, very thinly and finely velutinous toward the base in many specimens, but in our Florida material never seen with white tomentum at the base, as described by Bresadola, solid or stuffed, 5–12 x 1–1.5 mm. — *Context* pallid, very brittle when dried, tender when fresh; *odor* very slightly farinaceous, almost inodorous in most cases; *taste* distinctly farinaceous but not bitter.

Spores 6–7 x 3.5–4 μ, smooth, with eight or less longitudinal flattenings bordered by obtuse or almost rounded edges, not or hardly visible even in chloral hydrate but the outline of an optical section clearly octagonal (or hepta- or hexagonal) when the longer diameter of the spore is pointing up toward the objective (like an egg seen "from above"), fusoid to ovoid, hyaline to stramineous-hyaline, at least the larger spores with a suprahilar depression, non-amyloid; *basidia* 16–25 x 6.8–8.3 μ; *cystidia* and *cheilocystidia* none; *gill trama* partly intermixed; all *hyphae* without clamp connections.

Habitat: Widely scattered on sandy places, in May and June (June and July in Italy).

Distribution: With certainty known only from Italy and north Florida, probably widely distributed but easily overlooked since it is rare and small, and often occurs in places where commonly no fungi are expected.

Material studied: **Fla.:** Alachua Co., Gainesville, June 1943, *R. Singer, F 2294* (FH); May 1943, *W. A. Murrill, det.* R. Singer, *F 2072* (FH). — **Italy: authentic**, from Gocciadoro, province of Trento, July 1899, *G. Bresadola* (NY).

Among the smaller species of *Clitopilus*, sect. *Scyphoides*, this species is well-determined by its color and the more or less central stipe, its occurrence on sunny, sandy places in spring. There is a minor difference between our Florida material and the Italian plant, i.e. the lack of the white tomen-

tum on the base of the stipe of the former. This is an interesting parallelism to what we have observed in the following species, *C. scyphoides*. In neither case should too much importance be attributed to this frequently variable character. Otherwise, our specimens agree perfectly with the authentic material cited above. *C. Giovanellae* is new for this continent.

8. **Clitopilus scyphoides** (Fr.) Sing. comb. nov. (*sensu lato*).

Agaricus scyphoides Fr., Syst. Mycol. **1:** 163. 1821 (equals var. *typicus* f. *typicus*).
Agaricus mutilus Fr., Syst. Mycol. **1:** 191. 1821 (equals var. *typicus* f. *mutilus*).
Omphalia scyphoides Quél., Champ. Jura, p. 99. 1872.
Pleurotus mutilus Gill., Champ. Fr. Hymen., p. 344. 1878.
Omphalina scyphoides Quél., Enchir., p. 42. 1886.
Clitopilus submicropus Rick, Broteria, **6:** 77. 1907 (equals var. *submicropus*).
Omphalina floridana Murr., Mycologia **33:** 440. 1941 (equals var. *floridanus*).
Pleuropus minimus Murr., Lloydia **5:** 144. 1942 (equals var. *floridanus*).
Clitopilus omphaliformis Joss., Bull. Mens. Soc. Linn. Lyon **10.** 1941 (*fide* Locquin, *ibid.* **13:** 107. 1944).

Var. **typicus** forma **typicus**

The European type of this species does not occur in Florida, but it is here redescribed for comparison with the American varieties. Pileus white, convex and umbilicate or infundibuliform from the beginning, not hygrophanous or subhygrophanous but with a dry, sericeous, very thin and sometimes indistinct sericeous covering, eventually undulate but with more or less regularly circular outline, 5–25 mm. broad. Hymenophore white to creamy white, eventually pallid to pinkish in fertile specimens, separable from the context of the pileus, lamellae narrow (up to 1.5 mm. broad), arcuate or horizontal-linear, or descendant, always decidedly and mostly deeply decurrent, subclose to crowded. Stipe white, slightly sericellous, typically short, 4–10 x 0.5–1.8 mm. (up to 2 mm. at the typically white tomentose, frequently thickened base), equal or subequal, flexuous or straight (typically more frequently flexuous), solid or stuffed, becoming hollow in age. Context white, thin; odor farinaceous or none; taste farinaceous and mild. Spores ellipsoid-oblong, or in smaller spores with a rhomboid outline, typically narrower than in var. *floridanus*, 7.5–11.5 x 4–5.5 μ, otherwise as in the variety; basidia mostly 4-spored, 17–28 x 6.5–8.5 μ; cystidia and cheilocystidia none; trama as in var. *floridanus*; cuticle of appressed, long, cylindric, smooth, clampless, 2.5–3.5 μ thick hyphae, making up the sericellous covering; neither the spores nor the hyphae are amyloid.

Habitat: Solitary or in small to large groups in moist or mossy meadows or fields, but also on the soil or on very decayed stumps in the woods, May to October, through most of Europe but I have never verified the indications from Siberia and South Africa. I have, however, made fresh collections in Bavaria, near Munich, where it is frequent in May and June on meadows, and I have examined the material in Lundell & Nannfeldt, Fungi Exsiccati Suecici (LE) as well as two specimens from the

Höhnel Herbarium (FH), one from Jenbach, *V. Höhnel B.2145*, one from near Trento, *F. v. Höhnel.*

Var. **typicus** f. **mutilus** (Fr. *l.c.*) Sing. comb. nov.

Clitopilus omphaliformis f. *calathinoides* Locquin, Bull. Mens. Soc. Linn. Lyon **13:** 107. 1944.

This form does not occur in Florida, but it is here redescribed for comparison with other forms and varieties, and because it has so often been misinterpreted. *Pileus* white, subhygrophanous, very slightly transparently striatulate when wet, not viscid, very minutely subfarinaceous-subsericellous, not circular but elongate in outline when old, often becoming lobate, tongue-shaped, or labiate-depressed, very eccentric to lateral, and in the latter case assuming the general appearance of *Arrhenia auriscalpium* (but larger), with initially incurved margin, 10–14 mm. broad. *Hymenophore* white, eventually somewhat pink, lamellae crisp, with rather obtuse edge when young, forked or simple, rather narrow, subrounded-attenuate or arcuate to the stipe, descendant-decurrent, close. *Stipe* white, solid, short white tomentose at the base, erect and straight, occasionally flexuous, very minutely mealy-sericellous, subequal, 5–17 x 1–1.5 mm. *Context* white, fragile, inodorous. *Spores* 6.8–8.5 x 3.5–5 μ as in the var. *floridanus*; *basidia* up to 26.5 x 5–8μ, 4–spored; *cystidia* and *cheilocystidia* none; *trama* intermixed, its bilaterality has not been checked by the author; hyphae without clamp-connections.

Habitat: On mossy north border of a mixed (*Pinus, Picea, Betula*) wood, growing among mosses (or actually on decayed needles scattered among these?).

Distribution: Certainly in Scandinavia, France, Finland, and also in the Leningrad region of the U.S.S.R., near Mga, August 21, 1938, *R. Singer & L. N. Vassilieva L37, 5–596* (LE). The above description was gathered from this latter collection. This form probably occurs in most of Europe.

Var. **floridanus** (Murr. *l.c.*) Sing.

PLATE I, FIG. 8–11.

Pileus white, pure white when dry, becoming sordid-pallid when old and wet, innately fibrillose-sericellous, smooth, or scarcely noticeably striatulate when wet, sometimes somewhat uneven, with the margin initially incurved, convex and umbilicate from the beginning, the umbilicus very deep, eventually the pileus deeply depressed, 8–20 mm. broad. — *Hymenophore* white or creamy white, eventually becoming pinkish in the fertile carpophores, easily separable from the context of the pileus, lamellae arcuate, decurrent to deeply decurrent, narrow (about 1 mm. broad), subclose to close, simple; spore print pale and dirty pink. — *Stipe* white, whitish, or sordid-pallid when old, glabrous or somewhat innately white-fibrillose, smooth, even, the base hardly noticeably mycelioid, versiform but usually as long as the pileus is broad, or longer, rarely shorter, and subequal, solid

or stuffed, sometimes becoming hollow, sometimes curved, 5–20 x 1–2.5 mm. — *Context* white, thin, very brittle when dried; odor farinaceous, or sometimes none; taste farinaceous, and slightly bitterish to mild.

Spores often agglutinate in fours, or in pairs, 6–10 x 3.7–5 μ, ellipsoid to ventricose-subfusoid, smooth, hexa- to octagonal because of (6)–8 flattened longitudinal ribs limited by obtuse or somewhat rounded edges which are not or hardly visible even in chloral hydrate, but become evident in an optical section with the long diameter of the spore pointing upward to the objective (like an egg seen "from above"), the wall thin and very easily collapsing, especially along the longitudinal edges, and then often appearing longitudinally ridged, some with a slight suprahilar depression, some only with an applanation, non-amyloid, hyaline to stramineous-hyaline; *basidia* 17–26.5 x (5)–6.7–9.5 μ, 4–spored, sometimes some 2– to 3–spored; *cystidia* and *cheilocystidia* none, but in some specimens many basidia abortive; *gill-trama* intermixed- subbilateral, non-amyloid, the hyphae without clamp connections; *cuticle* of the pileus (the thin silky covering) consisting of long, cylindric, appressed, smooth, more or less interwoven, clampless hyphae of 2–5.3 μ diameter, forming a loose to subdense tissue.

Chemical reactions: **$FeSO_4$,** somewhat grayish, almost negative. — **Methylparamidophenol,** negative.

Habitat: On open lawns, on bare ground and among grasses, also on roadsides and near the hammocks, never in the hammocks, fruiting from May to October. Gregarious.

Distribution: Common all over Florida.

Material studied: **Fla.:** Dade Co., Miami SW, 15th Road, October 1942, *R. Singer F 1216/II* (FH); Highlands Co., Highlands Hammock State Park, August 1942, *R. Singer F 465* (FH); Alachua Co., Gainesville, several collections, among them **type** of *Omphalina floridana, W. A. Murrill F 16223* (FLAS); and **type** of *Pleuropus minimus* Murr., *W. A. Murrill, F 19980* (FLAS, FH).

Var. **submicropus** (Rick *l.c.*) Sing. comb. nov.

Pileus as in var. *floridanus*, but more distinctly sericeous or sericeous-fibrillose, smooth, convex with depressed center, larger, 20–30 mm. in diameter. — *Hymenophore* as in var. *floridanus*, close to crowded, sometimes somewhat forked; spore print pale and dirty pink. — *Stipe* white or pallid, innately fibrillose to somewhat mealy, especially on the apex, smooth, the bases connected by a very thin mycelioid membrane, solid, equal, but frequently with slightly thickened base and apex, sometimes flexuous, 10–25 x 2–4 mm. — *Context* white, very brittle when dried and also more or less fragile when fresh, rather thin; odor farinaceous; taste slightly bitter to mild.

Spores often agglutinate in pairs or in four, 5.5–6.8 x 3.5–4 μ, shaped as in var. *floridanus*; *basidia* 17 x 6.8 μ; *cystidia* and *cheilocystidia* none seen; *hyphae* without clamp connections.

Habitat: In the hammocks (tropical hammock formations in Florida), on small debris and sticks, gregarious to cespitose, fruiting in Florida in October.

Distribution: Tropical Florida and Brazil, possibly all over tropical America.

Material studied: **Fla.:** Dade Co., Matheson Hammock, October 1942, *R. Singer F 1252* (FH). — **Brazil: type,** Rio Grande do Sul, 1906, *J. Rick* (FH).

Rick indicates the spores as being 6 x 2.5 μ, but in the type specimens I have found many foreign spores as well as many collapsed spores of the *Clitopilus*, and some of these fit in Rick's measurements. However, the non-collapsed spores of Rick's specimen perfectly agree with the above measurements taken from my Florida collection.

Var. aff. **floridanus,** ined.

Pileus as in the type variety but less distinctly sericellous. *Hymenophore* as in the type variety but often sterile. *Stipe* as in the type variety but less silky, more elongate in general and more frequently straight, sooner becoming hollow in large specimens, 3–17–(24) x 0.7–2 mm., the base glabrous in some specimens, white tomentose in others (inconstant). *Context* white, not very fragile, but very brittle when dried; odor farinaceous only when the carpophores are squeezed. *Spores* 7.7–9 x 4.5–5.2 μ (specimen from North Dakota); *basidia* 17.5–27.5 x 6.5–8.5 μ, 2–, 3–, or 4–spored (very variable); *cystidia* and *cheilocystidia* none; *trama* and *cuticle* as in var. *floridanus*.

Habitat: On well-watered lawns on the soil, also in swamps on decayed leaves and wood, and on burned-over prairie sod, fruiting from June to August, gregarious.

This is another form, close to var. *floridanus* (Murr.) Sing., but obviously not entirely identical with it, found in the northern and western states.

Material studied: **Vt.:** Middlebury, July 1897, *E. A. Burt* (FH). — **Mass.:** Woburn, August 1943, *W. L. White, det.* Singer (*sterile form*) (FH). — **N.D.:** Kulm, June 1923, *J. F. Brenkle* (under a new unpublished name), N. Dakota Fungi *1613*.

Sect. **Pleurotelloides** Sing. sect. nov.

A sectione praecedente stipite inconstanter formato vel haud persistente aut rudimentario vel complete absente differt.

Characters of the section: these are evident from the key p. 551, and the above Latin diagnosis. Type species: *Clitopilus pleurotelloides* (Kühn.) Sing.

9. **Clitopilus venososulcatus** Sing. spec. nov.

Pileo pallide albo, radiato-sulcato et venoso, farinaceo, sessili vel subsessili, 12–23 mm. lato; lamellis concoloribus, satis angustis, postice attenuatis, confertis; sporis in cumulo roseolis, 8–8.5 x 4.5–5 μ, substramineis, striatulis; stipite nullo vel minutissimo, usque ad 1.3 x 0.6 mm.; carne inodora. Habitatio: Ad lignum emortuum prope Miami Floridae, U. S. A.

Pileus pallid white, radially venose and sulcate, mealy, not viscid, sessile or subsessile, 12–23 mm. broad. — *Hymenophore* white or pallid, becoming

dotted with pink from the spores, lamellae rather narrow (1.5–2 mm. broad), close, attenuate behind; spore print pinkish on white paper. — *Stipe* absent or rudimentary, and then concolorous and minutely mealy, not larger than 1.3 x 0.6 mm. — *Context* white, inodorous, very thin, very fragile.

Spores hyaline to pallid-stramineous, ellipsoid or short ventricose-subfusoid, or somewhat ovoid, longitudinally substriate because of flattened ribs limited by obtuse edges, in optical cross section obscurely angular, hexagonal or octagonal, 8–8.5 x 4.5–5 μ; *basidia* 20–21 x 7–7.5 μ; *cystidia* and *cheilocystidia* none seen; all *hyphae* without clamp connections.

Habitat: On dead portions of standing trunks of living *Ficus aurea*, and also on logs from the same host. October.

Distribution: Coastal Hammock in south Florida.

Material studied: **Fla.:** Dade Co., Matheson Hammock, October 29, 1942, *R. Singer F 1344*, **type** (FH).

This species is close to *C. pinsitus* (Fr.) Josserand and *C. pleurotelloides* (Kühn.) Sing. It differs from both in the venose surface, and from the latter species also in being larger.

10. **Clitopilus pleurotelloides** (Kühn.) Sing. comb. nov.

Octojuga pleurotelloides Kühner, Le Botaniste **17:** 158. 1926.
Octojuga variabilis (Fr. *sensu* Karst. p. p., *non al.*) Fayod, Ann. Sci. Nat., sér. VII. **9:** 390. 1889.
Clitopilus variabilis Josserand, Bull. Soc. Myc. Fr. **53:** 212. 1937.
Octojuga Fayodi Konr. & Maubl., Icon. Sel. Fung. **6:** 234. 1924–36.
Geopetalum viticola Murr., Bull. Torr. Bot. Club **67:** 2. 1940.
Pleurotus viticolus Coker, Journ. E. Mitch. Sci. Soc. **60:** 92. 1944.

Pileus pallid white, frequently becoming somewhat dirty grayish cream in age, opaque, white tomentose in the zone nearest to the substratum, smooth or transparently striatulate when moist, at least in the marginal zone when quite mature, glabrous but sericeous or finely villous when seen under a lens, circular, semicircular, or reniform, convex, sometimes attached by a resupinate portion and the free margin horizontally deflexed, the margin initially incurved, then repand and straight and occasionally radiately splitting, largest diameter of the non-resupinate portion of the pileus 1.5–10 mm. — *Hymenophore* pallid, lamellae moderately broad to very broad, subclose to rather distant, inserted, with entire or slightly uneven edges; spore print pale cinnamon pink. — *Stipe* absent, or present in very young specimens and then up to 1 mm. long, but soon becoming rudimentary and button-like, or entirely disappearing, concolorous, subpruinose to sericeous. — *Context* concolorous, very fragile, brittle when dried; odor none or very slight, farinaceous; taste mild.

Spores 5.5–9 x 3.5–5.8 μ (according to Kühner up to 12 x 6.2μ), stramineous-hyaline, non-amyloid, ellipsoid to ovoid in outline but slightly hexagonal, octagonal, or decagonal with flattened to very slightly concave sides when seen in optical cross section, from one end; *basidia* 25–29 x

7.5–8.5 μ, 4–spored or a few 2–spored; *cystidia* and *cheilocystidia* none; *trama* non-amyloid; *hyphae* of the sericeous covering of the pileus cylindric, subinterwoven with some semi-erect ends, 2–4 μ thick, all hyphae without clamp connections.

Habitat: On dead cortex of tree trunks, on logs and dead branches, vines, (*Quercus, Eucalyptus, Salix,* according to R. Maire, *Cornus florida* and *Vitis* spec. according to Coker), and also on fallen needles of conifers, dead thallus of mosses (*Hypnum* according to Kühner), on bark of *Zizyphus jujuba,* also on herbaceous stems; June to December.

Distribution: Europe, Asia, and America, possibly cosmopolitan but often overlooked or misdetermined.

Material studied: **Fla.: type** of *Geopetalum viticola,* Alachua Co., Arredonda, 1938, *Erdman West & W. A. Murrill* (FLAS). — **USSR:** (formerly Finland), Kellomäki, Sept. 1940, *R. Singer 5–836* (LE). — **India:** Ladhar, Sheikhupura, *Sultan Ahmed,* August 1944 (*det.* Singer), *1097* (FH).

Fayod based his name on an observation by Karsten, Mycol. Fenn. **3:** 112. 1876: "Occurrit forma sporis minoribus (longit. 6 mm., crassit. 3–4 mm.), subhyalinis, qvalem in ramulis *Salicis Capraeae* prope Åbo mense Aug. legimus." Åbo is now Turku, Finland, and it may be of interest that I collected this species in Finland (or what formerly was Finland) on debris of rotten moss among sand near the railway station of Kellomäki, September 1940. There is, therefore, little doubt that Fayod was right in attributing this variety to what we now call *Clitopilus pleurotelloides.* But the type variety of *Agaricus variabilis sensu* Karsten is, as I have been able to confirm on the basis of Karsten's exsiccatum of this species distributed by him under #511 of the Fungi Fennici, determined correctly in the sense of the majority of the authors, *i.e.* it is a typical *Dochmiopus* (Agaricineae) with rough spores. Kühner was, therefore, justified in erecting a new name for the *Clitopilus* reserving the epithet "*variabilis*" for the *Dochmiopus.* The American collections do not differ sufficiently to separate them from *C. pleurotelloides.* They are, perhaps, slightly thinner with the lamellae accordingly broader and the surface of the pileus accordingly more striatulate, but striations are frequent in European specimens also, and the size of the lamellae and the diameter of the flesh vary considerably. The spores are slightly smaller in the types than they are in the European specimens I have studied, but Coker, who has re-collected Murrill's form in North Carolina, gives spore measurements which are exactly intermediate to almost identical with my European measurements (6.7–9 x 4.8–5.8 for the Kellomäki collection, 5.5–8 x 3.5–4.8 μ for Murrill's type). This again shows that the size of the spores is variable in this country as well as in Europe, though not more so than in some other species of this same genus. Murrill observes that "not one individual was found entirely resupinate, nor was there a stipe in the entire lot." If this latter observation should hold true for all American collections, including the youngest stages, it would be possible to distin-

guish Murrill's species as a form or variety of *C. pleurotelloides*. I doubt very much that the astipitate character of the American form is constant since it is not constant in the European plant.

EXTRALIMITAL SPECIES

Clitopilus crispus Pat., Bull. Soc. Myc. Fr. **29:** 214. 1913.

The type has been described from Indo-China. These specimens and an excellent colored picture are preserved at the Farlow Herbarium. There is also a spore print on blue paper which when transferred on white paper now is between "fawn color" and "wood brown." The mature spores are stramineous under the microscope, or, in dense piles, succineous, ellipsoid with some tendency to become hexagonal, with seven to ten (mostly eight) angles reinforced by longitudinal ribs and with furrows between them when seen in an optical cross section from one end, the ribs projecting about 0.4 μ, 6.8–8.8 x 4.3–5.2 μ. This species is by far the stoutest of the small-spored *Clitopili*, but, nevertheless, belongs in the section *Scyphoides*.

Clitopilus orcelloides Pat. & Demange, Bull. Soc. Myc. Fr. **26:** 40. 1910.

The type, preserved in the Patouillard Herbarium (FH), comes from Indo-China. It has spores exactly as described by Patouillard, *i.e.* ellipsoid-subhexagonal or subrhomboid, or equally ovoid-ellipsoid, octagonal when seen from above, and then the angles reinforced by longitudinal veins which in the optical cross section look like knots, 5.5–7.5 x 3.7–5.3 μ, sometimes as short as 6 x 5.2 μ, the ribs projecting up to 0.3 μ; hymenium and trama not very distinct in these specimens. There is an excellent colored picture in the unpublished "album" of V. Demange, executed by a native artist, and representing the type specimens in fresh condition. These vividly recall *Clitopilus scyphoides* var. *floridanus* from which the dried specimens are difficult to distinguish. However, the more angular spores, many of which are ornamented with ribs, cause me to consider *C. orcelloides* a different though related species of the section *Scyphoides*.

Clitopilus Passeckerianus (Pilát) Sing., Mycologia **34:** 66. 1942.

Pleurotus Passeckerianus Pilát, Atl. Champ. Eur., *Pleurotus* Fr., Ser. A, **9–10:** 49. 1935.

Pleurotellus Passeckerianus Konr. & Maubl., Icon. Sel. Fung. **6:** 361. 1938.

Octojuga Passeckeriana Sing., Ann. Mycol. **40:** 61. 1942.

This is a frequent weed-fungus in white-mushroom beds, and in my opinion is slightly different from *C. pinsitus* as well as from *C. scyphoides* var. *typicus* f. *mutilus* and *C. pleurotelloides*. For more descriptive data see the original account of Pilát, (1935) with photographs, and also Singer, (1942).

SPECIES IMPERFECTLY KNOWN

Clitopilus pinsitus (Fr.) Josserand, Bull. Soc. Myc. Fr. **53:** 210. 1937.

Agaricus pinsitus Fr., Syst. Mycol. **1:** 184. 1821.

This species, originally described from Sweden, has been redescribed by Josserand from France. Though it is impossible to prove that Josserand's interpretation is the only correct one, it seems to me that it is the best emendation of an otherwise superfluous Friesian species. I have not collected it myself, nor has it been found in America. It differs from *C. pleurotelloides* in being much larger and in having close, narrow lamellae.

SPECIES DUBIAE

Clitopilus cretatus (Berk. & Br.) Sacc., Syll. **5:** 702. 1887.

Described from England, this species is thought by Lange to be the same as *Pleurotus mutilus, i.e. Clitopilus scyphoides* var. *typicus* fa. *mutilus*. However, R. Maire (Publ. Inst. Botàn. **3**(4): 83. 1937) refers it to his genus *Clitopilopsis* because of Massee's indication on the spores of the type specimen of *Agaricus cretatus* Berk. & Br., Ann. Mag. Nat. Hist. ser. III. **7:** 373. 1861. In Massee's paper (Grevillea **21:** 81. 1893) are some not quite trustworthy measurements, and it may be unwise to take his word for it that these spores are not of the *Clitopilus*-type. A reexamination of the types at Kew will decide whether *C. cretatus* is another synonym of *C. scyphoides*, or a good species in some other genus.

SPECIES EXCLUDENDAE

Clitopilus abortivus (Berk. & Curt.) Sacc., Syll. **5:** 701. 1887.

This species, common in north Florida in winter, does not belong in this genus, but must be called *Rhodophyllus abortivus* (B. & C.) Sing., Rev. d. Mycologie **5:** 9. 1940. Other species formerly called *Clitopilus*, but having angular spores of the *Rhodophyllus*-type, must also be placed in the genus *Rhodophyllus* rather than *Clitopilus*. These are *C. undatus* Fr. (*ut Agaricus*), *C. cancrinus* Fr. (*item*), *C. albogriseus* Peck (*item*) (*Rhodophyllus albogriseus* (Peck) Sing., *recte*), and many others.

Clitopilus pallidus Heim, Treb. Mus. Ciènc. Nat. Barcelona **15**(3): 109. 1934.

Since *Clitopilus* is now used in the sense of Patouillard and Maire, the species of *Clitopilus em.* Heim, *l.c.* must go into *Clitopilopsis* Maire (Agaricineae). The type species of *Clitopilopsis* is *C. pallida* (Heim) Maire from Spain. Another species to be excluded is *Clitopilus togoensis* Henn., also considered to belong in *Clitopilus em.* Heim by Heim (1934) and Singer (1936), and certainly belonging in the Agaricineae rather than in the Jugasporaceae.

GENERA EXCLUDENDA

The following genera formerly considered to be allied to the boletes or other groups of the Boletineae, are now excluded from this suborder.

Filoboletus Henn. (belongs to the Tricholomataceae, Agaricineae).
Polyporoletus Snell (belongs to the Scutigeraceae, Clavariineae).
Fistulina Bull. *ex.* Fr. (belongs to the Fistulinaceae, Cyphellineae).
Volvoboletus Henn. (is a parasitized or abnormal *Amanita*).

GENERA DUBIA

Fistulinella Henn.
Melanomphalia Lange.
Gymnogomphus Fayod.

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THE MOST IMPORTANT LITERATURE ON THE BOLETINEAE, ESPECIALLY THOSE OF FLORIDA

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EXPLANATION OF PLATE I

All figures are drawn at a magnification of × 2000.

Fig. 1–3. *Gomphidius rutilus* (Fr.) Lund. & Nannf. ssp. *alabamensis* (Earle) Sing.

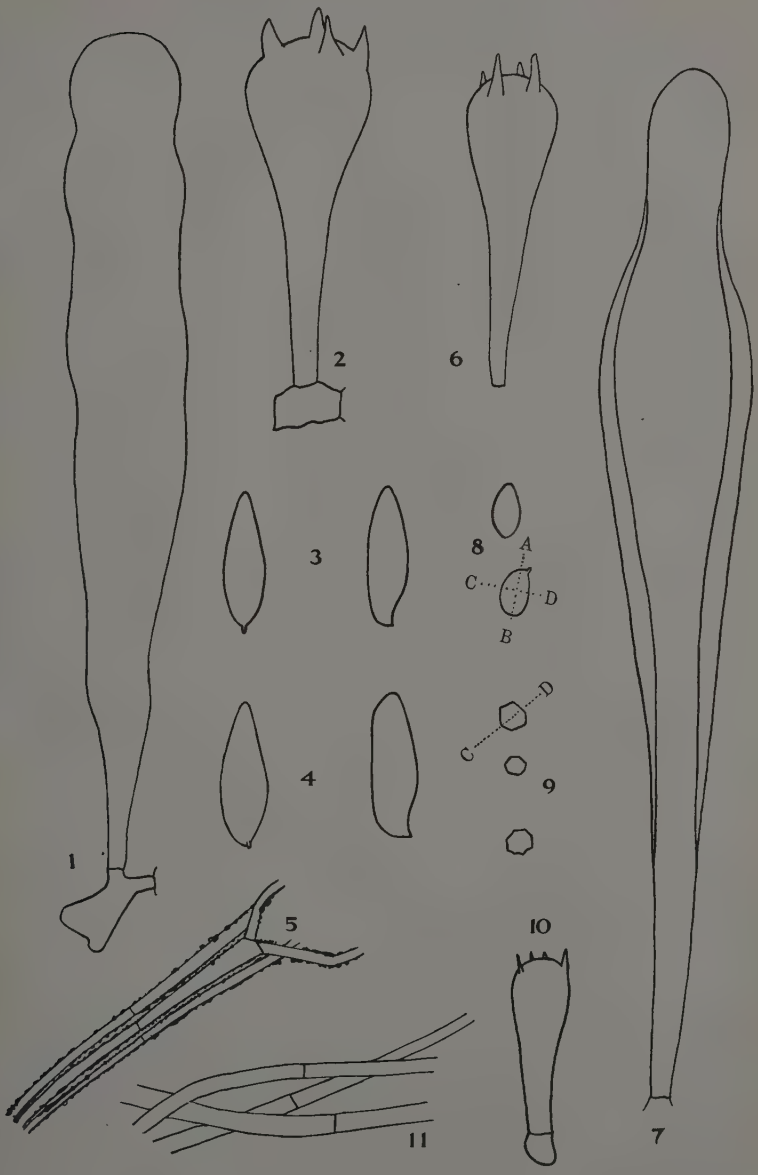
1. Cystidium.
2. Basidium.
3. Two spores, (left) frontal view; (right) in profile.

Fig. 4–7. *Gomphidius vinicolor* Peck ssp. *jamaicensis* (Murr.) Sing.

4. Two spores, (left) nearly-frontal view; (right) in profile.
5. Hyphae of the remainders of the veil on the apex of the stipe, running in parallel strands, with strong pigment-incrustation.
6. Basidium.
7. Cystidium with the partially thickened wall.

Fig. 8–11. *Clitopilus scyphoides* (Fr.) Sing. var. *floridanus* (Murr.) Sing.

8. Two spores, (above) in frontal view; (below) in profile with the hilar end above; the line A . . . B indicates the longitudinal axis, C . . . D the short axis.
9. Three spores, seen from above (the longitudinal axis A . . . B vertically directed toward the lens), the short axis indicated corresponding to fig. 8, lower spore, as C . . . D. The upper spore shows 6 flattened sides and 6 angles, central one 7, the lowest 8 (which is the normal number in this form).
10. Basidium.
11. Hyphae of the sericeous covering of the pileus.



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